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FINAL REPORT

PART 1 of 2

A Description and Numerical Analysis of the Factors Affecting the Processes of Production in the Gulf of Alaska

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Acknowledgments

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SUMMARY

Objective 1. To conduct a search and present a compilation of available baseline biological and associated physical and chemical data from the Gulf of Alaska (planktonic realm).

Conclusion: The data have been compiled and submitted to NODC on magnetic tape.

Implications: Measurement of the effects of petroleum development will depend upon comparison of data with pre-development figures (i.e., those of this study).

Objective 2. To use the compiled data for a description of the temporal and geographic variation in phytoplankton standing stock (and species), production, and related physical and chemical factors.

Conclusion: Annual, seasonal, geographic, and vertical variation of biological and associated factors has been described in the pelagic realm of the eastern Subarctic Pacific. Annual and seasonal features are dominant. Geographic variation is limited to differences between coastal and oceanic regimes.

Implications: Evidence of natural fluctuations in plant biomass and production are now available for comparison with changes related to petroleum development. Grazing and circulation patterns indicate the possibility of long-term toxins (hydrocarbons) in the food chain leading to salmon.

Objective 3. To use the data from Station "P" in a model of phytoplankton productivity and to test the sensitivity of the model to changes in physiological constants and external parameters.

Conclusion: A model has been completed arid the results are sensitive to more of the inputs during the winter than during periods of high grazing pressure in the spring.

Implications: The model may be used to relate natural and oil-related changes in the environment to plant production.

INTRODUCTION

A. General nature and scope of study

A study of the potential impact of modifications to an ecological system must determine both the quantity and distribution of organisms and the relationship between these various organisms. Baseline studies are necessary in order to assess the average stocks in an area and the natural variations within these stocks. Knowledge of the energetic which relate the different organisms is also necessary in order to estimate changes which might be expected from modifications of the system. Even more important, a general understanding of the gross processes controlling the ecological system, when applied to a simple model, is an invaluable tool in designing and implementing the baseline studies. This study encompasses the pelagic ecosystem in the Gulf of Alaska, concentrating on the first step of the food chain.

B. Specific objectives

The specific objectives of this study are:

1. To search the existing literature and unpublished data in order to compile baseline information on factors of importance to phytoplankton production.
2. To synthesize the baseline information into a description of the seasonal and geographic distribution of phytoplankton standing stock, production and related physical and chemical factors insofar as the existing data are suitable.
3. To use the data to initialize a numerical model and to determine the combinations of process submodels which lead to distributions in the dependent variables that are in agreement with observations.

4. To test the sensitivity of the results of the "standard" run to changes in the submodels and independent variables; identify those variables and processes which strongly influence the results.

c. Relevance to problems of petroleum development

The results of this study are relevant to petroleum development in two ways: First, the baseline information which we have compiled may be used (where the existing data are suitable) to compare effects after petroleum development with the natural range of values in the pelagic ecosystem. Second, we can suggest the types of modifications to the plant community which might be associated with a large scale oil spill.

This study describes the "normal" state of the ecosystem in the Gulf of Alaska, as well as any natural fluctuations of plant populations that have occurred in the past. Where the data are adequate, comparisons with this norm should be the basis of any future study of the actual impact of petroleum development on the pelagic ecosystem. We can now point out areas in which we feel the data are lacking. The model results from Station "P" indicate the variables which most strongly influence primary production. It would stand to reason that these variables should also be gathered in any further studies in the Gulf of Alaska if they are not already available.

It is obvious that, with the exception of the area around Station "P", there are insufficient data in the Gulf of Alaska to describe quantitative cause and effect relationships. Individual species of phytoplankton are likely to be most sensitive to chemical changes in the environment so that changes in species distribution may be good indicators of changes in the ecosystem. This study describes those species distributions that have been found in the past.

To actually predict the effects of an oil spill on the primary producers is a task far beyond the capabilities of the present study. To do this, one would need supporting information on the effect of oil on the physical properties of the water column and on the physiology of the plants and animals. Still, we can suggest the nature of the changes which might occur. For instance, a layer of oil on the sea surface may be expected to decrease the transmission of light and the transfer of turbulent energy across the air-sea interface. This can be modeled by decreasing the incident radiation and by reducing the vertical mixing. This same layer of oil might affect the plant community by decreasing the maximum production rate and by increasing the respiration rate (an artificial means of increasing mortality). We have tried the above demonstrations in order to evaluate the value of this scientific model as a management tool.

The effects of an oil spill on the productivity of underlying waters would be, for the most part, short term effects. There is also a possibility of long term effects of petroleum development in the Gulf of Alaska. One such long term effect would be the introduction of different oil fractions into the food chain. Some of these fractions may not be toxic to organisms low on the food chain, but could be toxic to man. For instance, high boiling aromatic hydrocarbons are suspected as long-term poisons, perhaps carcinogenic ones, and the nonhydrocarbon fractions of crude oil behave in a similar manner (Blumer, 1969).

In the Gulf of Alaska during the spring bloom, it has been reported that grazing by a large stock of herbivores keeps the phytoplankton standing stock at a constant level (McAllister *et al.*, 1960). If an oil spill were dispersed into tiny droplets either chemically or by wave action, these droplets would likely be consumed along with the living cells. Circulation patterns described

in the literature we have reviewed show, in addition to the counterclockwise flow around the Gulf of Alaska, that currents flow north from the Alaskan stream through the Aleutians to Bristol Bay (Figure 24). Thus, hydrocarbons consumed by zooplankters would be distributed to one of the main feeding ground of salmon, and chemicals of unknown but suspected toxicity to man could become concentrated in a major food source.

PHYTOPLANKTON PRODUCTIVITY MODEL

A. Abstract

The objectives of this numerical study of primary productivity at Ocean Station "Papa" (Station "P") are:

1) to provide a quantitative synthesis of the ideas which have been advanced concerning plant production;
2) to assess the relative importance of the various processes which contribute to net plant production; and
3) to speculate about the consequences of environmental changes to the standing stock of the plants.

We synthesized one combination of biological concepts to simulate the observed chlorophyll distributions and plant productivity over the course of one year. This model was then used to study the sensitivity of the results to changes in some of the model inputs. It was also used to simulate the effects of environmental changes on the plant community. With the present uncertainty about the input values and the processes which govern phytoplankton distribution, there may be other, equally valid models. Two of the least-known independent variables, the carbon-to-chlorophyll ratio and the zooplankton feeding threshold, both exert a major influence on the results throughout the year and are exceedingly important for part of the year.

B. Current state of knowledge

Observations which have been made concerning primary production at Station "P" indicate that: 1) chlorophyll concentrations show very little change throughout the year (Parsons and LeBrasseur, 1968); 2) nutrients (nitrogen) are available in sufficient quantity so as not to limit plant growth (Anderson *et al.*,

1969); 3) plant production in the water column, however, peaks during the early summer (McAllister, 1969) ; and 4) this excess production must be cropped down by the grazers (McAllister, *et al.*, 1960).

Figure 1 is a composite of the surface chlorophyll data (McAllister, 1962; Stephens, 1964, 1966, 1968, 1970) for the years from 1959 to 1970. All of the data are plotted against the day of the year, regardless of the actual year. In this and all other figures, day 1 corresponds to January 1. Ail chlorophyll concentrations measured before 1963 were assumed to be over-estimates. These values had been computed using the formulae of Richards with Thompson (1952) or Strickland and Parsons (1960). We multiplied these values by 0.76 to make them compatible with the equations of Parsons and Strickland (1963) and UNESCO (1966) . The correction factor is taken from Banse and Anderson (1967). It is obvious from these data that there is considerable variation in the surface chlorophyll values at any given time of the year. The mean chlorophyll concentration, however, may not change much throughout the year.

Not only do the chlorophyll concentrations vary at the surface, but there is also considerable scatter in their values at depth. Because of this, the data for these 12 years were averaged into blocks covering 30 days and 10 m in depth in order to present a mean description of the chlorophyll-depth profile as it changes throughout the year. Figure 2 shows the average data and the standard deviation of the data. Values which are enclosed by a dotted circle are each derived from only one data point and, therefore, have no standard deviations associated with them. There are also no data for certain depth intervals. In Figure 2, we also pass a hand-fit curve through the mean data.

Figure 3 shows the seasonal, depth variation of the mean chlorophyll distribution. The *twelve* smoothed curves from Figure 2 were used in generating Figure 3. The top figure illustrates the time and depth dependence of

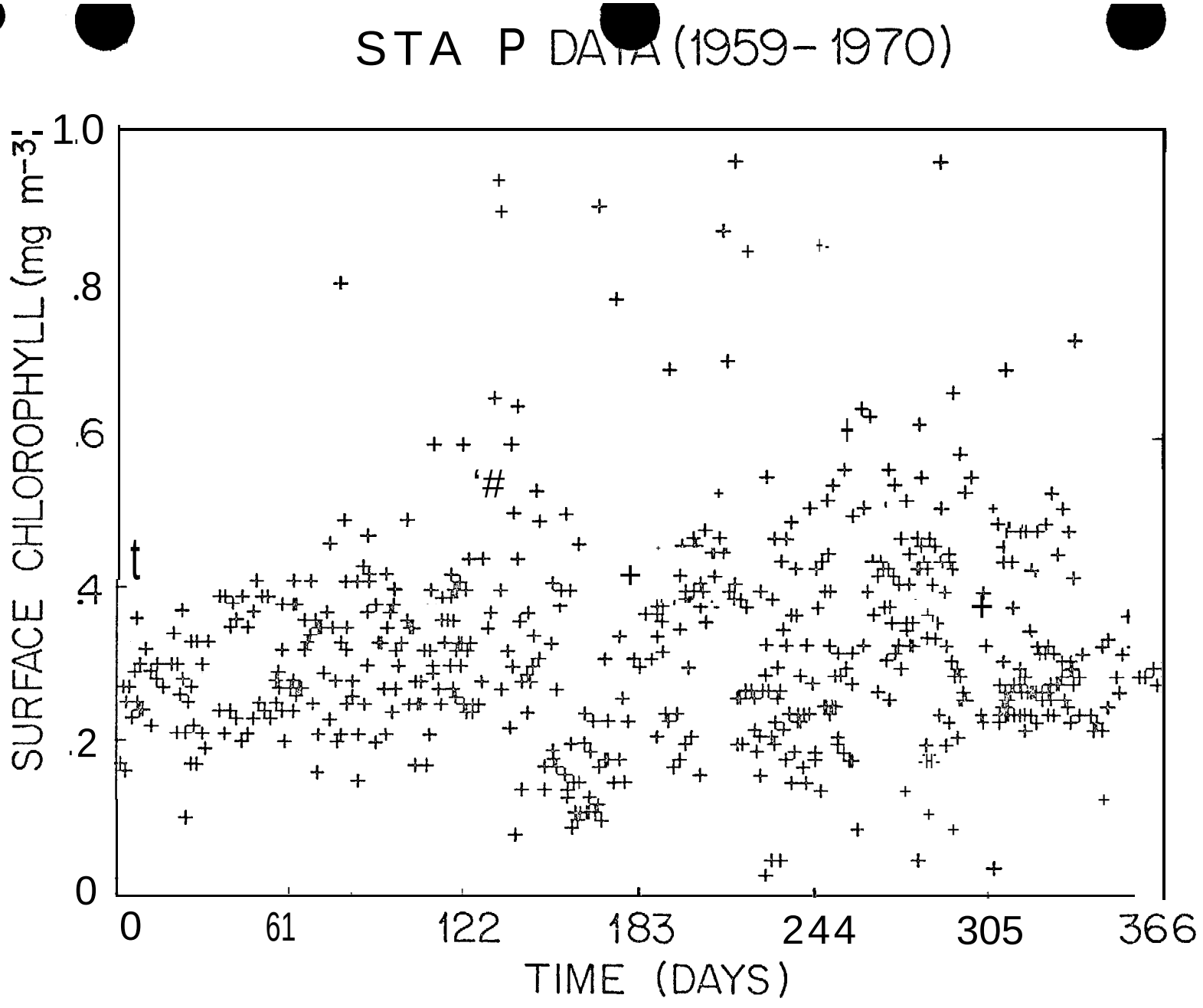


Figure 1. Surface chlorophyll values at Station P. Data from all the years are combined.

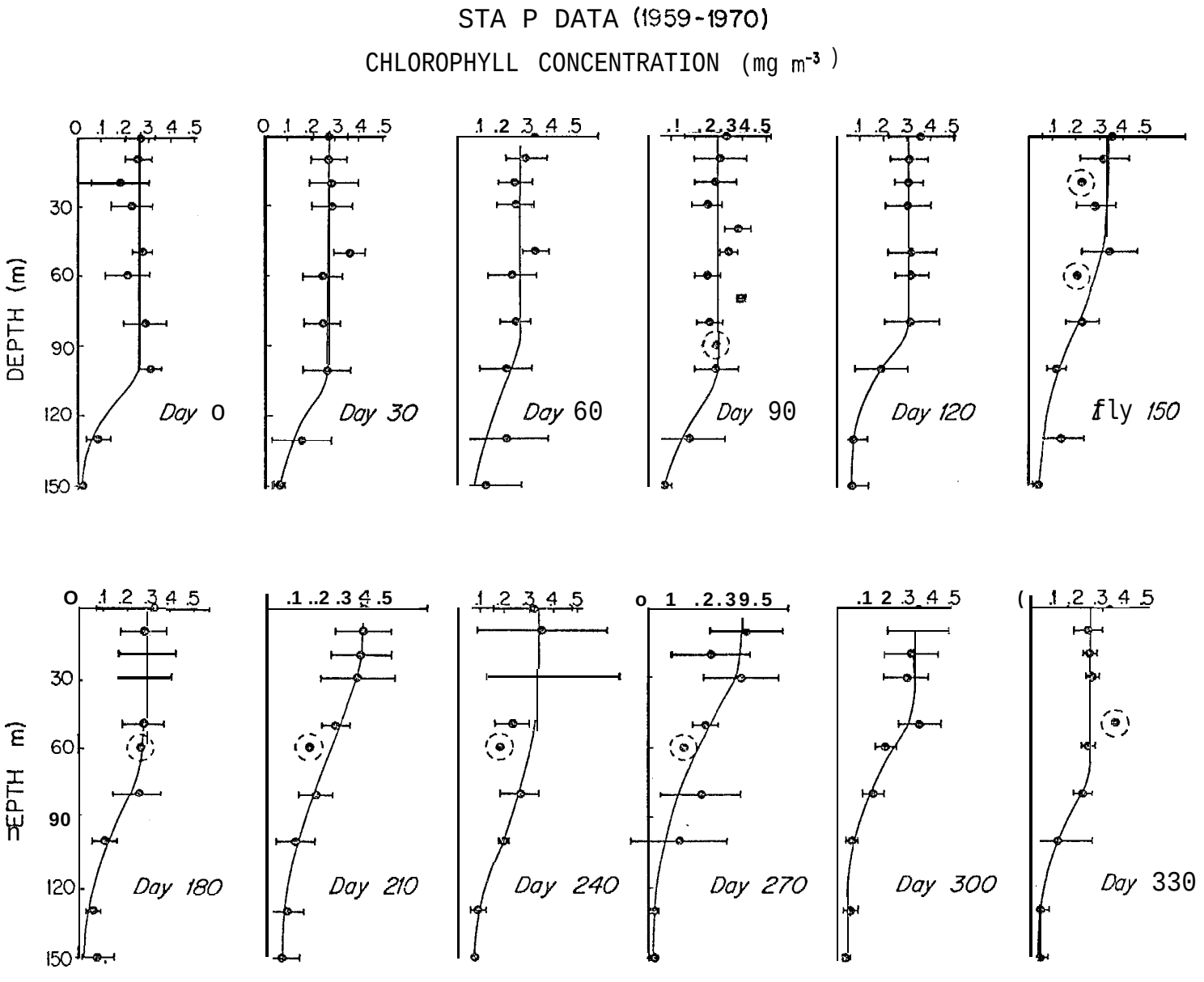
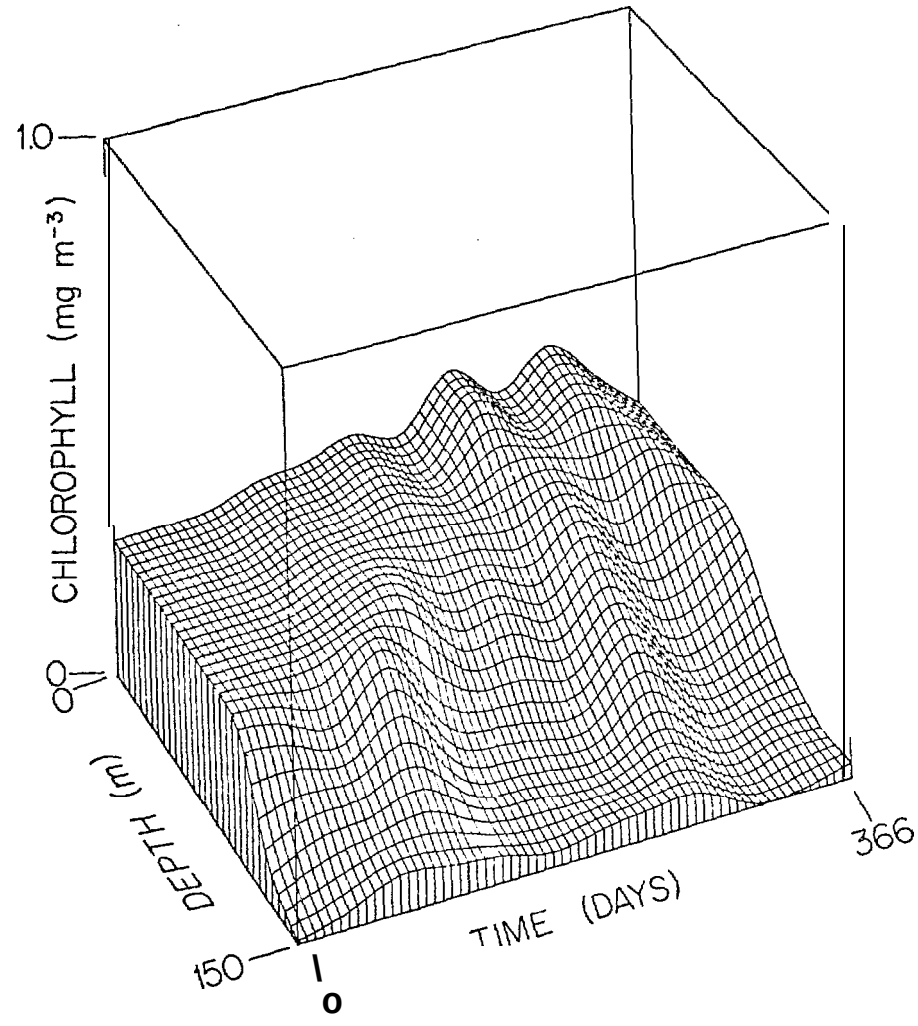
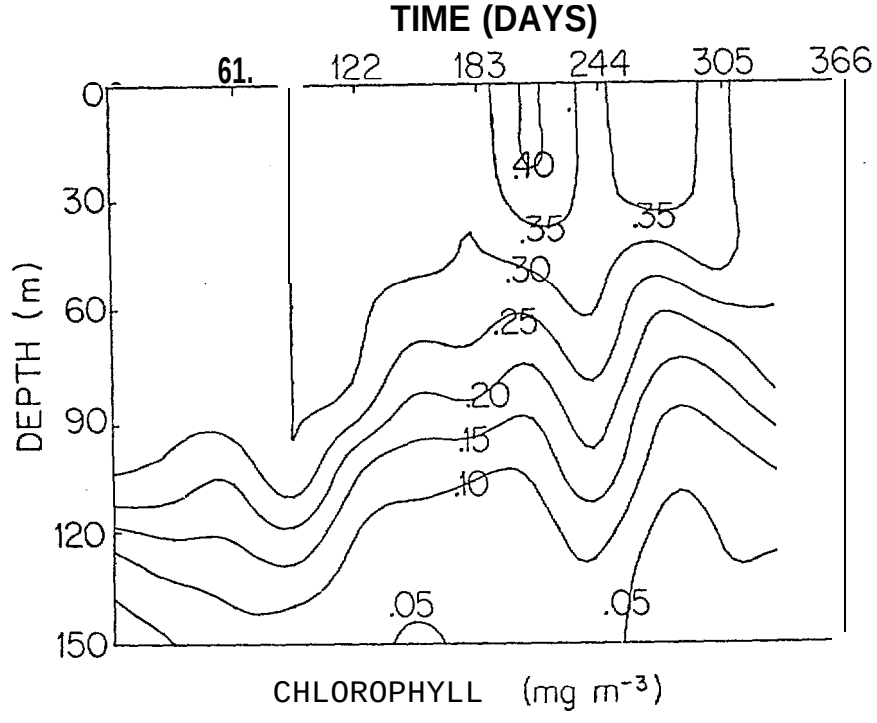


Figure 2. Mean (30 day-10 m blocks) chlorophyll concentration. Error bars indicate standard deviations. Dotted circle surrounds the "mean" values when only one data point is available. Hand-fit curves are shown for these data.

Figure 3. Mean, seasonal and depth variation in chlorophyll concentration. Data from hand-fit curves in Figure 2. Top, 3-dimensional representation. Bottom, contour plot.


1.0
CHLOROPHYLL (mg m⁻³)
0
DEPTH (m)
150
0
TIME (DAYS)
366


TIME (DAYS)
61.
122
183
244
305
366
0
30
60
90
120
150
DEPTH (m)
.40
.35
.35
.30
.25
.20
.15
.10
.05
.05
CHLOROPHYLL (mg m⁻³)

chlorophyll concentration. The bottom figure presents the same information in a contour plot. Here the contours are for values of constant chlorophyll. It may be seen from either of these figures chat the change in chlorophyll concentration with season is relatively small in the near surface waters. The chlorophyll concentrations in the mid-depths do show more variation as the mixed layer depth changes from summer to winter.

Nitrate data for Station "P" are available for the six years from 1965-1970 (same source *as* chlorophyll data). Figures 4 and 5 show the mean profiles and the seasonal depth variation for this nutrient. Surface nitrate reaches a high of about 17 $\mu g\text{-at } \ell^{-1}$ in the winter and is reduced to a low of about 7 $\mu g\text{-at } \ell^{-1}$ in the late summer. Even the minimum value encountered in the summer is sufficiently high so that nitrate is not limiting phytoplankton growth. It is interesting to note that nutrients are being removed from the near surface waters throughout the year and that the minimum surface nutrients in the summer occur at about the same time as the maximum surface chlorophyll concentrations.

Values for the integrated carbon production in the water column are only reported for the three years, 1961 to 1963. The depth to which production was measured and hence integrated varied somewhat throughout the data. That depth, however, was not less than *50* m and the small amount of production which was neglected below the integration depth would not have greatly changed the reported values. The time variation of production in the water column is shown in Figure 6. This composite description shows a peak in production about the end of June.

Station "P" has a very complete coverage of the seasonal variation in zooplankton biomass (LeBrasseur, 1965). The data on the zooplankton wet weight were obtained by net hauls from *150* meters to the surface. The values, however,

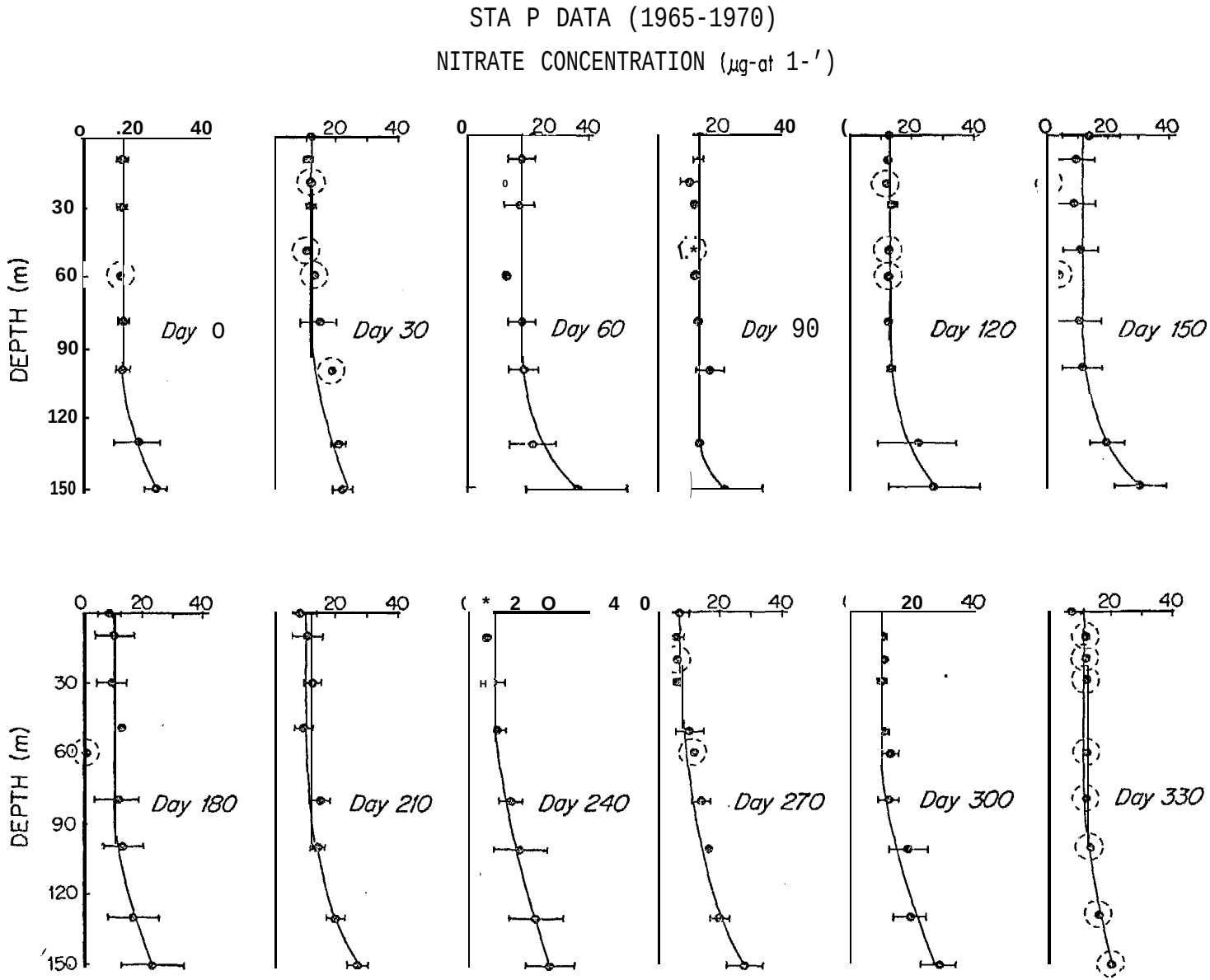
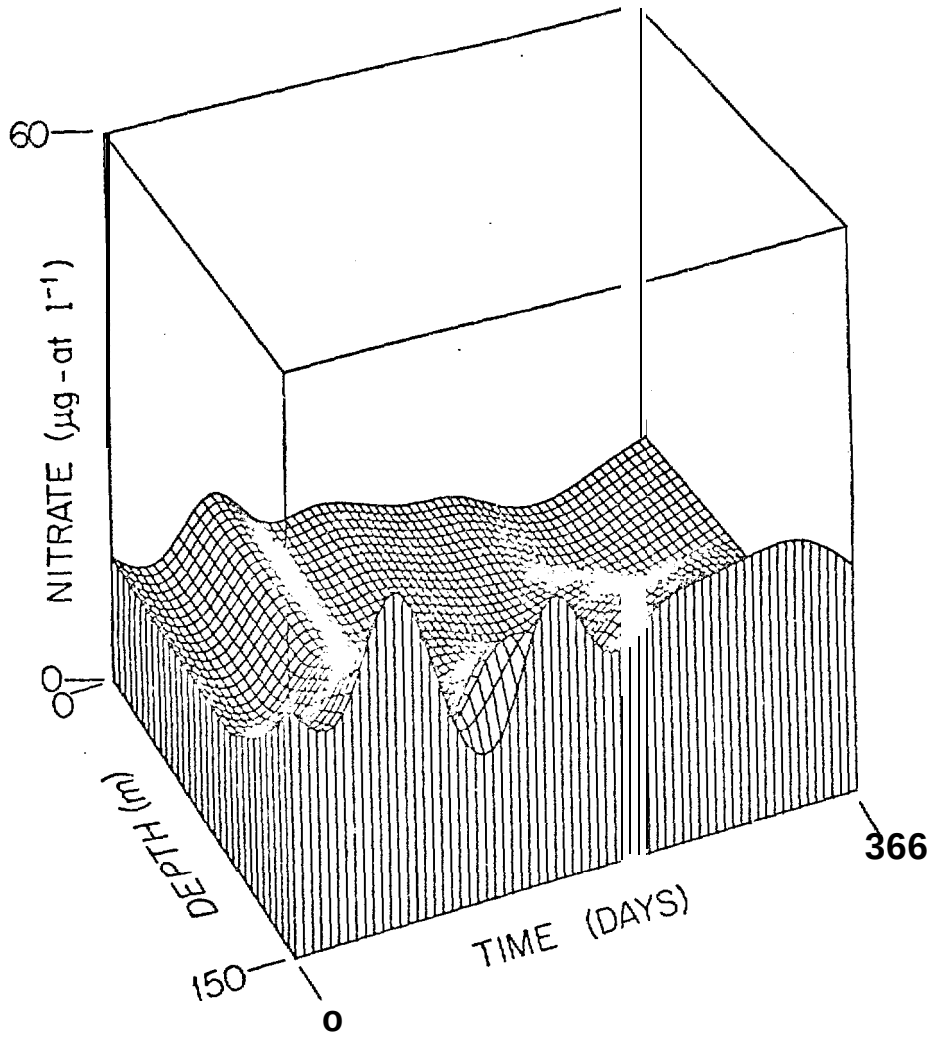
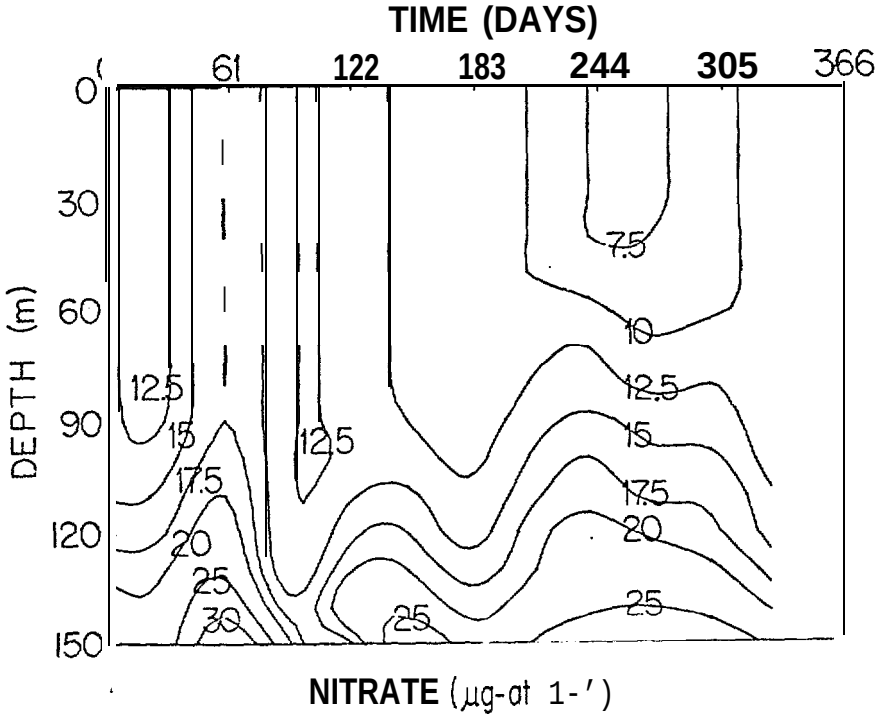


Figure 4. Mean (30 day-10 m blocks) nitrate concentration. Error bars indicate standard deviations. Dotted circle surrounds the "mean" values when only one data point is available. Hand-fit curves are shown for these data.

Figure 5. Mean, seasonal and depth variation in nitrate concentration. Data from hand-fit curves in Figure 4. Top, 3-dimensional representation. Bottom, contour plot.


60
NITRATE (µg-at l⁻¹)
0
DEPTH (m)
150
0
TIME (DAYS)
366


TIME (DAYS)
0
61
122
183
244
305
366
DEPTH (m)
30
60
90
120
150
7.5
10
12.5
15
17.5
20
25
30
NITRATE (µg-at 1-')

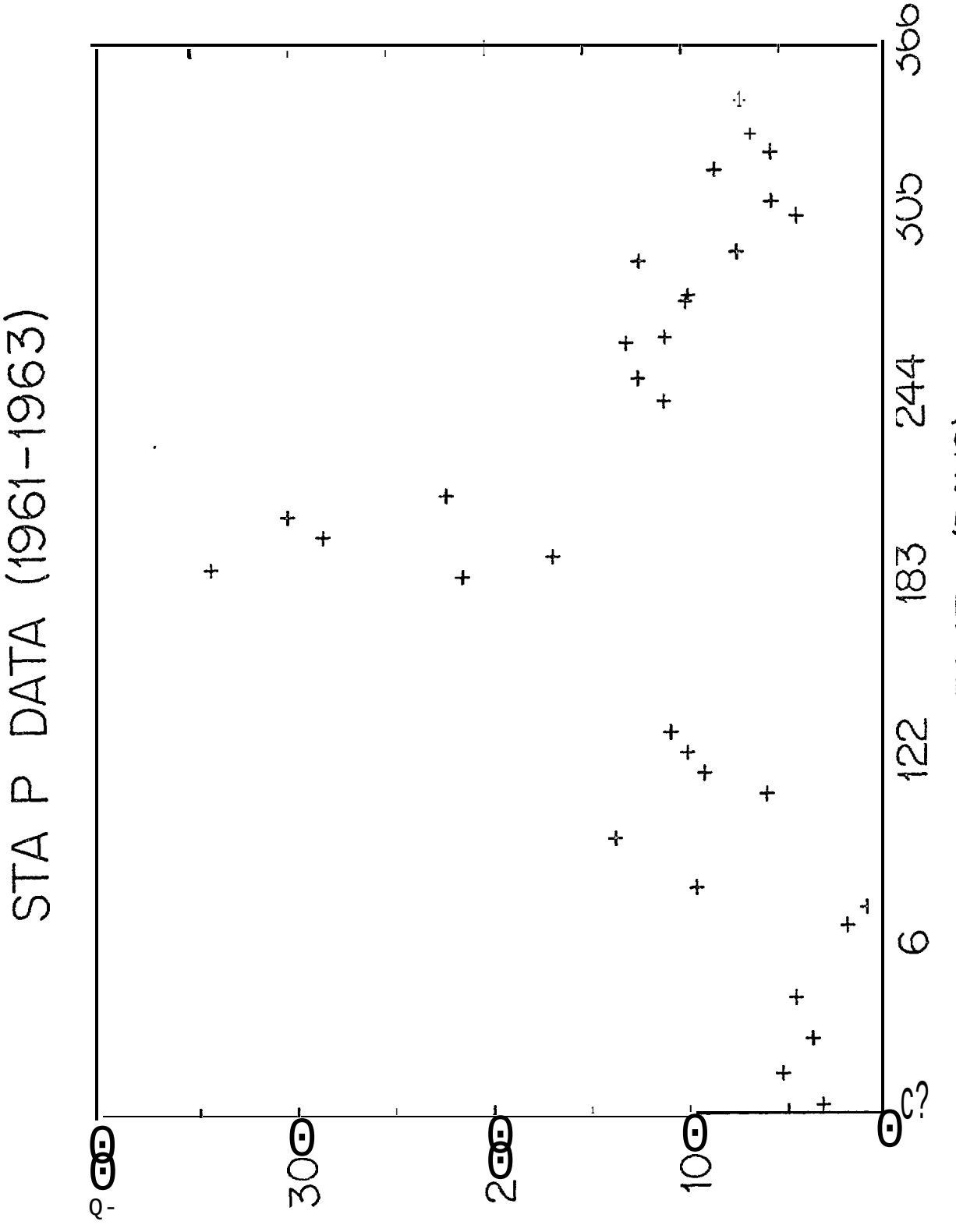


Figure 6. Daily production in the water column.

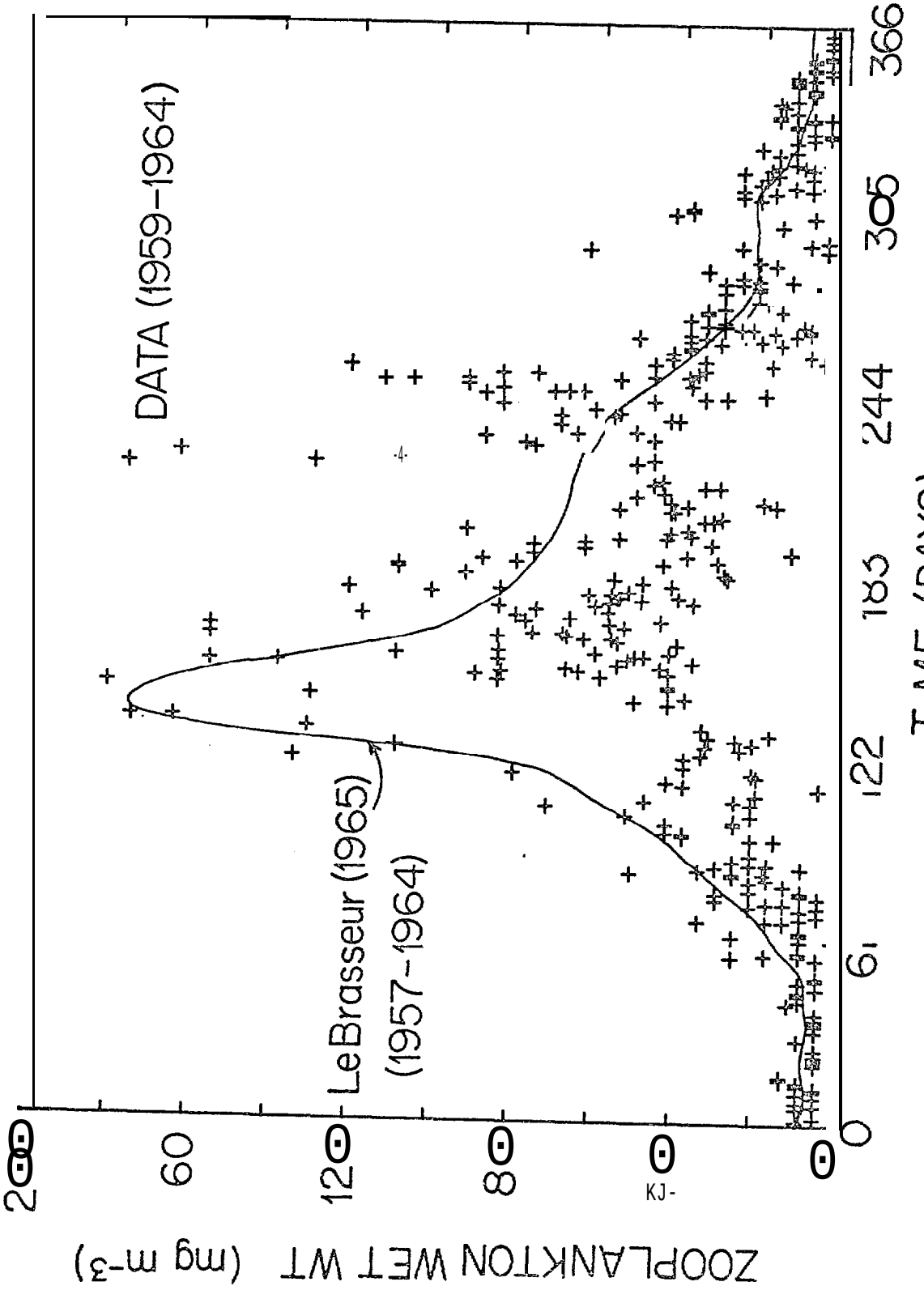


Figure 7. Seasonal zooplankton wet weight data and an averaged curve. Values given are means in the top 150 m of the water column.

are reported as concentrations per unit volume so that those values must be multiplied by the volume of the 150 m deep water column in order to arrive at the zooplankton biomass of the water column Figure 7 shows both the data (1959 to 1964) and an average curve for 1957 to 1964 (LeBrasseur, 1965) for zooplankton wet weight.

c. Study area

Weather Station "P" has been chosen as the study area because of the extensive time series of biological and physical data collected there.

D. Model equations and inputs

It is one goal of this study to combine the observations at Station "P" with theories concerning plant production in order to study the processes of primary production which are occurring at that location. To that end, we will construct a model to describe chlorophyll concentrations and check our theories by comparing the results of this model with observations. In the model, we begin with an initial chlorophyll-depth profile and simulate the change in that profile with time. The time rate of change in chlorophyll depends on 'processes such as mixing and sinking, on net production, and on grazing. In general, net production and grazing both depend, in turn, on the chlorophyll concentration. For instance, production depends on the supply of limiting nutrients, which is governed, itself, by the uptake and regeneration due to the phytoplankton. Similarly, the grazing pressure is proportional to the number of herbivorous zooplankters and that zooplankton population depends on the availability of plant food. Thus, a description of plant production should consist of three coupled equations; one describing the rate of change of the plants, one the rate of change of the nutrients, and one the rate of change of the population of grazers. However, because nutrients do not limit production at Station "P", they may be eliminated from the model. Also, because of the large amount of zooplankton biomass data and because of the uncertainties associated with trying to describe zooplankton growth, we feel that it is better to use the zooplankton data as an independent input in place of the zooplankton growth equation.

This simplifies the model to one equation describing the rate of change of plant material (chlorophyll), which does not depend on the external nutrient concentration and which includes zooplankton biomass as one of the independent inputs. While this simplification is justified by the observations at Station "P",

it does limit the generality of the model. For instance, it is unrealistic to allow this model to produce a massive phytoplankton bloom since we know that such a situation would deplete the available nutrients and necessitate a consideration of the effects of low nutrients on production. Likewise, if the plant population were to drop to very low levels in the model, it is unlikely that the system would be able to support the observed zooplankton population. So, this would violate our assumption that zooplankton grazing pressure may be modeled by the measured zooplankton biomass.

The advantage of this simplified model is that it allows us to simulate the biological system at Station "P" with a minimum of assumptions concerning biological processes, many of which are poorly understood at present. The disadvantage, as mentioned in the previous paragraph, is that we cannot apply this model to extreme situations. In the following sections, we will present the equations governing the rate of plant production and the constants and independent variables used in those equations.

The rate of change of chlorophyll depends on mixing and sinking, on gross production, and on grazing by the herbivorous zooplankton. Thus, it may be expressed as:

$$\partial_t A = \partial_z (K \partial_z A) - w \partial_z A + \left[P_{max} \tanh\left(\frac{I\alpha}{P_{max}\gamma} \right) - R \right] A - \frac{G}{\gamma} \left\{ 1 - e^{-\beta (A\gamma - P_o)} \right\}_1 \quad (1)$$

where:

$A(z,t)$ - chlorophyll concentration [mg m^{-3}]

$K(z,t)$ - vertical eddy diffusion coefficient [$m^2 s^{-1}$]

w - sinking speed [ms^{-1}]

P_{max} - maximum photosynthetic rate [s^{-1}]

$I(z,t)$ - light intensity [cal $cm^{-2} hr^{-1} \equiv$ ly hr^{-1}]

$\gamma(z,t)$ - carbon to chlorophyll ratio [mg-C (mg chl)$^{-1}$]

α — initial slope of photosynthesis vs. light curve [mg-C (mg-chl)$^{-1}$ ly^{-1}]

R - respiration rate [s^{-1}]

G(z, t) - grazing pressure [mg-C m^{-3} s^{-1}]

β - normalized initial slope of grazing curve [m^3 mg-C^{-1}]

$P_o(t)$ - feeding threshold [mg-C m^{-3}]

t - time [s]

Z — depth [m]

The boundary conditions on the chlorophyll concentration are that there is no flux at the top (z = 0) and zero gradient at the bottom of the modeled water column ($z = z_{btm}$).

$$K \partial_z A - wA = 0 \qquad z = 0 \tag{2}$$

$$\partial_z A = 0 \qquad (z = z_{btm}) \tag{3}$$

Furthermore, it is assumed that there is a "near-surface" mixed layer, the depth of which (d_{mix}) varies with the time of year. Within the mixed layer, the governing equation for the rate of change of chlorophyll becomes:

$$\partial_t A = \frac{1}{d_{mix}} \left\{ [K \partial_z A - wA]_{d_{mix}} - [K \partial_z A - wA]_o + \int_0^{d_{mix}} \left| \left[P_{max} \tanh \left(\frac{I \alpha}{P_{max} \gamma} \right) - R \right] A - \frac{G}{\gamma} \left[1 - e^{-\beta (A\gamma - P_o)} \right] \right| dz \right\}$$

Invoking the surface boundary condition, this becomes:

$$\partial_t A = \frac{1}{d_{mix}} \left\{ (K \partial_z A - wA)_{d_{mix}} + \int_0^{d_{mix}} \left[P_{max} A \tanh \left(\frac{I \alpha}{P_{max} \gamma} \right) - RA - \frac{G}{\gamma} \left[1 - e^{-\beta (A\gamma - P_o)} \right] \right] dz \right\}, \qquad z \leq d_{mix} \tag{4}$$

In both equations 1 and 4, the grazing pressure is zero when $A < P_o \gamma^{-1}$.

Light intensity at depth in the water column depends on the amount of light at the surface of the water and the extinction of that light as it passes through the water column. So:

$$I(z,t) = I_o(t) e^{-c_1 z - c_2 \int_0^z A(z',t)dz'} \tag{5}$$

where:

$I_o(t)$ - light at the sea surface [ly]

c_1 - extinction coefficient of the water [m^{-1}]

C_2 - extinction due to self shading by the plants [$m^2 (mg\text{-}chl)^{-1}$]

The light penetrating through the sea surface depends on the amount of light reaching the top of the atmosphere, the amount which is lost in trar.smission through the atmosphere and the reflective losses at the sea surface. Thus :

$$I_o(t) = Is(t)_S \tau^{\sec \lambda} \tau_C^{\sec \lambda} \delta \tag{6}$$

where the solar radiation reaching a unit horizontal and at the top of the atmosphere is given by:

$$Is(t) = Jo \cos \lambda \tag{7}$$

where:

$$\cos \lambda \equiv \sin \phi \sin\text{-}9 + \cos \phi \cos \theta \cos h \tag{8}$$

$\sec \lambda = (\cos \lambda)^{-1}$

τ_S - transmission coefficient of the atmosphere

τ_C - transmission coefficient of the clouds

δ - fraction of solar radiation penetrating through the sea surface

Jo = 1.94 [ly rei^n-l] - solar constant

ϕ = 50 [deg] - latitude

h - sun's hour angle [deg]

$$\theta = 23.433 \cos\left[\frac{(d-174)\pi}{182.5}\right] - \text{sun's declination [deg]} \qquad (9)$$

d - day of the year

Sunrise and sunset are assumed to occur when cos $\lambda = 0$.

This model of chlorophyll. standing stock includes six independent variables: $K(z,t)$, $d_{mix}(t)$, $\tau_c(t)$, $\gamma(z,t)$, $G(t)$, $P_o(t)$, which must be specified. There are also 9 constants which must be supplied: w, P_{max}, α, R, β, τ_s, c_1, c_2, δ. In the following paragraphs, we will describe the choice of independent variables and constants which are used in the standard run.

Mixing Coefficient, K, and mixed layer depth, d_{mix}

The first term on the right-hand side of equation (1) is the contribution of turbulent mixing to the change in chlorophyll concentration at any depth. That mixing is parameterized by the vertical eddy diffusion coefficient, a value which is very poorly known for the oceans. Models of primary production have usually assumed constant values for this coefficient or have guessed at its time and depth variations. Station "P" is unique in having numerous measurements of physical and chemical parameters in addition to a large set of biological data which have been acquired over the years. If we assume that chlorophyll and temperature are both "mixed" by the same processes, then the temperature data may be used to calculate an apparent mixing coefficient for use in the biological model. Because of the extensive amount of temperature data which is available, we restricted ourselves to the data for 1970 (deJong *et al.*, 1971; Minkley, 1971; Garrett, *et al.*, 1971; Linggard, *et al.*, 1971; Gantzer and Healey, 1971) instead of averaging data from many years. That year was chosen because it was one of the earlier ones for which temperature measurements were available every month.

All of the temperature casts which reached a depth of 300 m were used in our analysis. Those data were blocked into monthly average values for certain depth intervals (see Table 1). The averaged temperatures were then fit by the functions:

$$T = T_0 + T_1 (e^{-a_1 z^m} - 1) - T_2 z; \qquad z \leq z_m \tag{10}$$

$$T = T_3 + T_4 e^{-a_2 z} - T_5 z \qquad ; \qquad z \geq z_m \tag{11}$$

where T and $\partial_z T$ are continuous at $z = Z_m$.

Values for T_3, T_4, and T_5 and a_2 were estimated from all of the temperature data since the temperature-depth profiles of the deep waters did not change significantly over the course of the year. z_m, T_0, T_1, a_1, m, T_2 were then chosen each month such that the continuity conditions at $z = z_m$ were satisfied and so that the curve best fit the monthly averaged temperature data. The temperature-depth profiles, as described by equations 10 and 11, for each month are given in Figure 8.

In order to calculate the mixing coefficient for heat (and by assumption also for chlorophyll), we start with an equation describing the rate of change of temperature in a diffusive medium (Carslaw and Jaeger, 1959);

$$\rho c \partial_t T = \partial_z (k \partial_z T) \tag{12}$$

where:

T - temperature [°C]

ρ - density [g cm^{-3}]

c - specific heat [cal $g^{-1}°C^{-1}$]

k - thermal conductivity [cal $cm^{-1}sec^{-1}°C^{-1}$]

Equation 12 may be rewritten as (assuming ρ and c do not vary with depth)

$$\partial_t T = \partial_z \left(\frac{k}{\rho c} \partial_z T \right)$$

$$= \partial_z (K \partial_z T)$$

Table 1. Monthly Average Temperature (“C), 1970

Month	Jan.	Feb.	Mar.	Apr.	May	June	July*	July†	Aug.	Sept.	Oct.	Nov.	Dec.
Number of cases	7	10	8	6	9	8	9	16	9	10	11	3	9
Depth (m)													
0	5.71	5.34	5.33	5.37	6.01	7.70	8.89	9.62	10.62	11.65	11.15	9.02	6.89
10	5.71	5.34	5.31	5.37	5.98	7.68	8.67	9.59	10.60	11.64	11.12	8.97	6.80
20	5.72	5.34	5.29	5.36	5.95	7.56	8.48	9.39	10.47	11.62	11.12	8.98	6.89
30	5.71	5.33	5.28	5.35	5.93	7.34	8.26	8.85	10.18	11.48	10.90	8.90	6.85
50	5.70	5.33	5.26	5.28	5.75	6.65	7.49	7.50	7.85	7.78	8.15	8.97	6.80
75	5.68	5.32	5.20	5.20	5.38	5.48	5.58	5.60	5.78	5.68	5.50	5.08	6.38
100	5.02	5.10	5.02	5.03	5.04	5.01	4.93	4.94	5.06	4.93	4.92	--	4.89
125	4.02	4.10	4.18″	4.20	4.34	4.46	4.48	4.57	4.59	4.57	4.67	4,36	4.49
150	4.02	4.08	4.07	4.05	4.10	4.26	4.12	4.16	4.19	4.26	4.33	4.25	4.32
175	3.91	3.97	3*99	3.96	3.99	4.12	3.97	4.01	4.04	4.09	4.18	4.17	4.19
200	3.79	3.85	3.88	3.85	3.88	3.98	3.86	3.91	3.95	3.98	4.07	4.09	4.05
225	3.73	3.77	3.80	3.77	3.81	3.89	3.79	3.82	3.86	3.90	3.99	--	3.97
250	3.70	3.72	3.75	3*73	3.77	3.83	3.74	3.77	3.81	3.84	3.92	3.92	3.93
300	3.66	3.68	3.71	3.68	3.71	3.74	3.69	3.71	3.72	3.75	3.83	3.81	3.80

* First half of month

† Second half of month

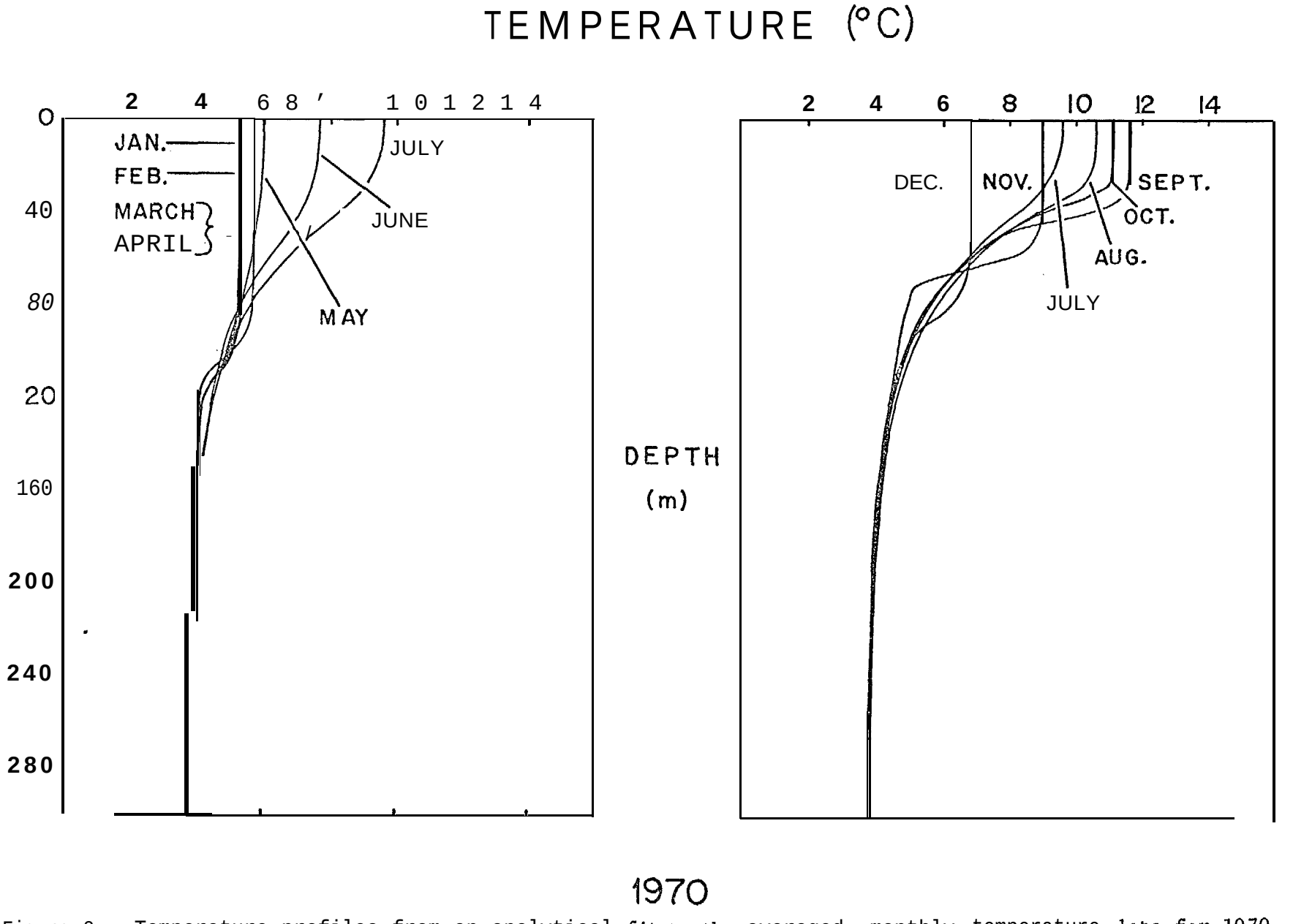


Figure 8. Temperature profiles from an analytical fit to the averaged, monthly temperature data for 1970.

where $K = k\rho^{-1}c^{-1}$ has the units of the eddy diffusion coefficient. For simplicity, we assume that the temperature distribution in the water column is at steady state so that:

$$\partial_z (K \partial_z T) = 0 \qquad (13)$$

Equation 13 is satisfied if K is proportional to $(\partial_z T)^{-1}$:

$$K \alpha (\partial_z T)^{-1}$$

The averaged temperature profiles (Figure 8 and equations 10 and 11) were used to calculate $\partial_z T$ for each month and equation 14 was then applied in order to get the functional form for K (Figure 9). The proportionality constant in equation 14 was estimated by 1) comparing our mixing coefficients (Figure 9) for the months of May through October with those of Vo Van Lanh (1974) and 2) "comparing our results with heat flux measurements at Station "P" (Tabata, 1961). The values for the diffusion coefficient which we used for the deep waters is presented in Figure 10.

The temperature data suggested that the near surface waters were subjected to convective overturn so that a diffusive description of mixing was incorrect for those waters. Thus equation 4 was developed for this near surface, mixed layer. The mixed layer depth changed with the season, and we estimated it from the temperature data. During the summer months, the surface waters would warm up during the day but would be mixed to some depth upon cooling during the night. This latter depth was taken as the mixed layer depth. The mixed layer depth is also shown in Figure 10, and no values of eddy diffusion are shown for the mixed layer.

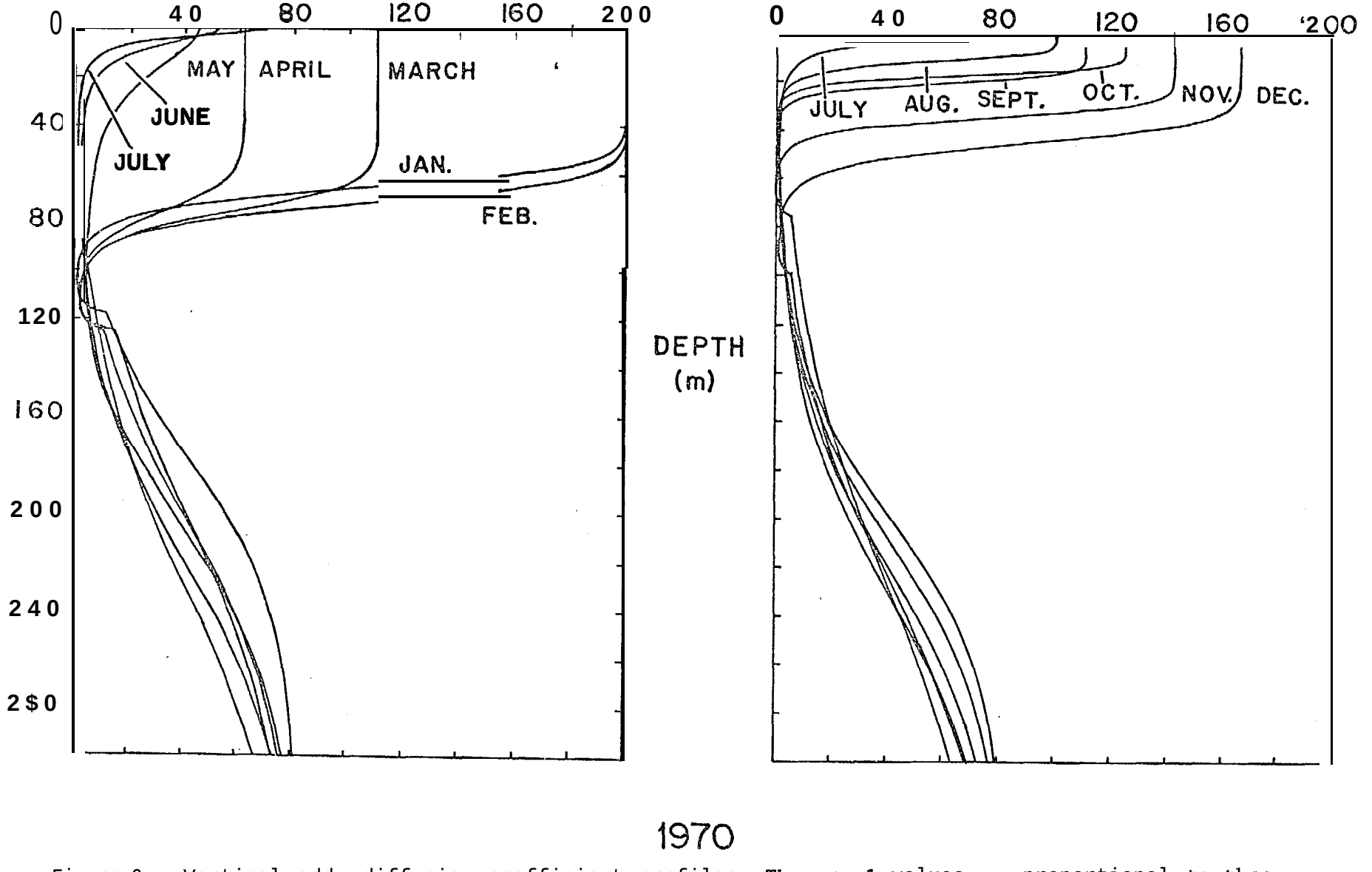


Figure 9. Vertical eddy diffusion coefficient profiles. The actual values are proportional to these curves and are shown in Figure 10.

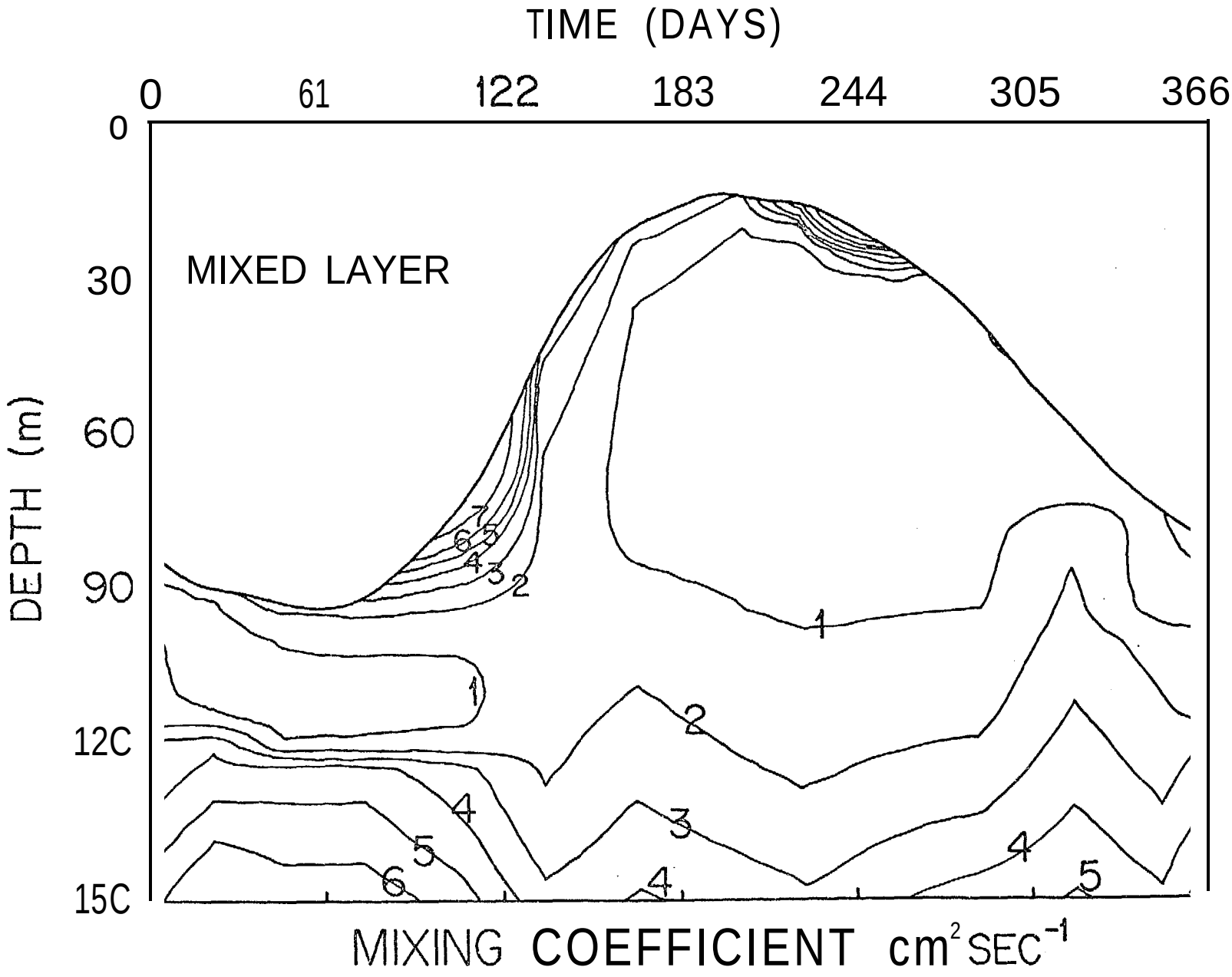


Figure 10. Vertical eddy diffusion coefficients "and the mixed layer depths for one year.

Cloud transmission τ_c

Monthly radiation data for the years 1960 to 1967 were obtained from Monthly Radiation Summary, Meteorological Branch, Department of Transportation, Canada. Figure 11 is a plot of the average daily radiation and the standard deviation in that value for each month of the year. In most cases, the standard deviation is no more than the size of the dot which was used to mark the mean values. These data were interpolated to every day of the year and the cloud transmission coefficients were adjusted so that the daily radiation in the model matched the data.

Carbon to chlorophyll ratio, γ

The carbon-to-chlorophyll ratio is difficult to measure (Banse, personal communication); yet, it is known to vary with both depth and season. Furthermore, we will show later that the modeled chlorophyll distribution is quite sensitive to changes in this ratio. For purposes of the standard run, we assumed that the carbon-to-chlorophyll ratio at the surface, $\gamma(0,t)$ varied as (McAllister, 1969):

$$\gamma(0,t) = 0.5\left\{65 - 35 \cos\left[\frac{2\pi}{365}(d-15)\right]\right\}$$

This results in a minimum surface value of 15 on the 15th day of the year and a maximum value of 50 on the 197th day. In addition, we assumed that the carbon-to-chlorophyll ratio at 150 m was always 10. $\gamma(z,t)$ was assumed to be uniform throughout the mixed layer and to approach a value of 10 at 150 m:

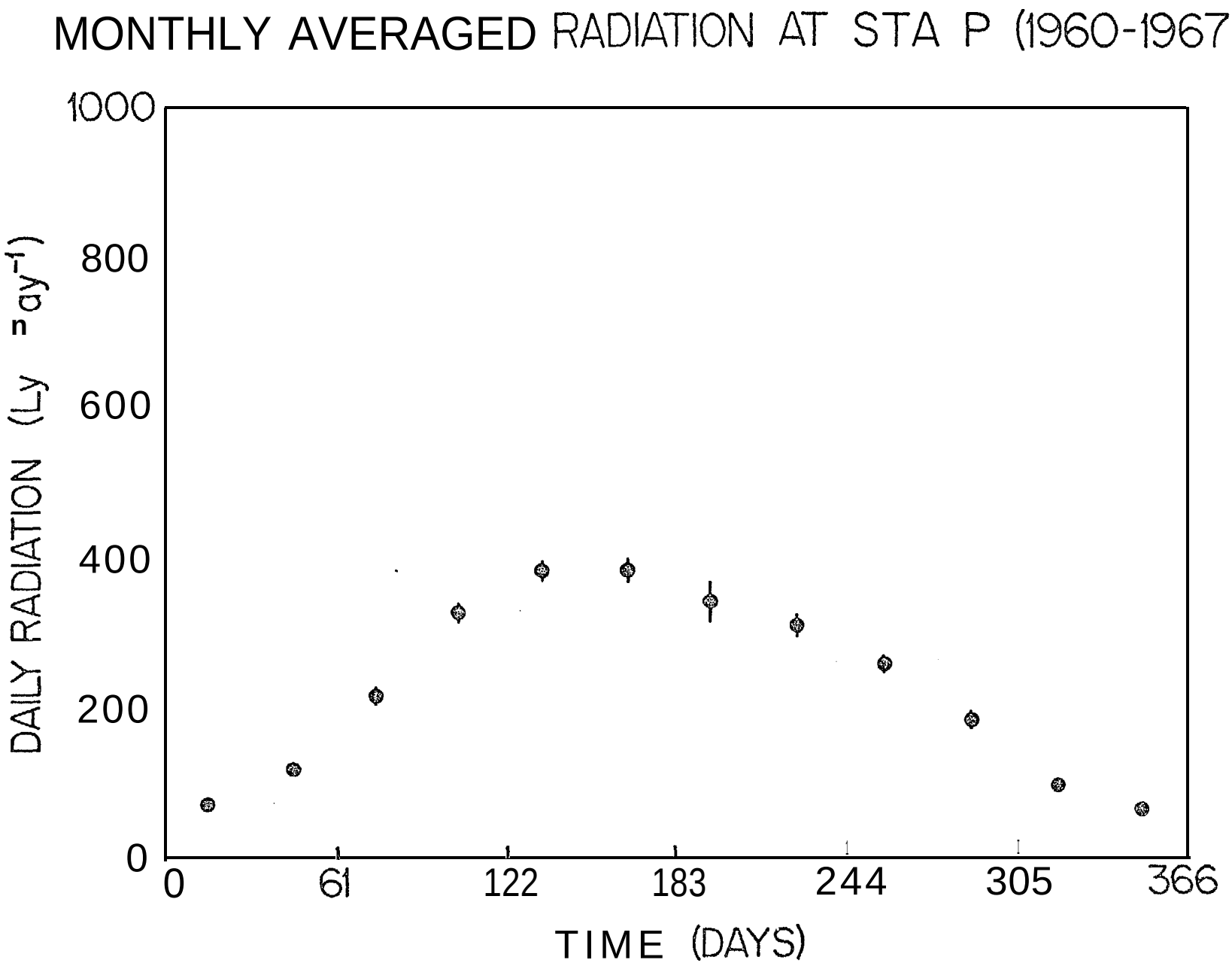


Figure 11. Average daily radiation received at Station P for each month of the year. The vertical lines give the standard deviation.

$$\gamma(z, t) = \gamma(0, t) \; ; \qquad z \leq d_{mix}$$

$$= 10 + (\gamma(0, t) - 10)e^{-b_1(\Delta z)^2} \; , \qquad z \geq d_{mix}'$$

where $Az = z - d_{mix}$ and $b_1 = \frac{6.91}{(150 - d_{mix})^2}$ is chosen so that $e^{-b_1(z')^2} = .001$ when $z' = 150m - d_{mix}$. The depth dependence of $\gamma(z,t)$ is shown schematically in Figure 12, while Figure 13 is a contour plot of the depth and time dependence of the carbon-to-chlorophyll ratio which was used in the standard run.

Grazing pressure, G, and feeding threshold, PO

The seasonal variation of zooplankton biomass is based on the average wet weights reported by LeBrasseur (1965) (Figure 7). These values were increased by a factor of 2.6 to correct for undersampling and the loss of small animals through the mesh (LeBrasseur and Kennedy, 1972). For most of the year, much of the zooplankton biomass consists of copepods, and we use a conversion factor of .6 mg-C/1.5 mg animal wet weight (Frost, personal communication), which would be appropriate for C. Plumchrus, Stage IV, in order to convert the biomass data to units of zooplankton carbon. It was necessary to assume that each animal exerted a maximum grazing pressure of twice its weight in carbon during a day. The resulting seasonal distribution of grazing pressure, G, is shown in Figure 14.

At any given time, the zooplankton are assumed to have a depth distribution which corresponds to that of their food, the phytoplankton. A comparison of the zooplankton depth distribution for 1957 (McAllister, 1961) with chlorophyll depth profiles suggests that the animals do tend to be distributed as assumed.

The feeding threshold, P_0, was adjusted to produce a standard run where the chlorophyll concentration and primary production are reasonal approximations to the observations. Those P. values are shown in Figure 15. A

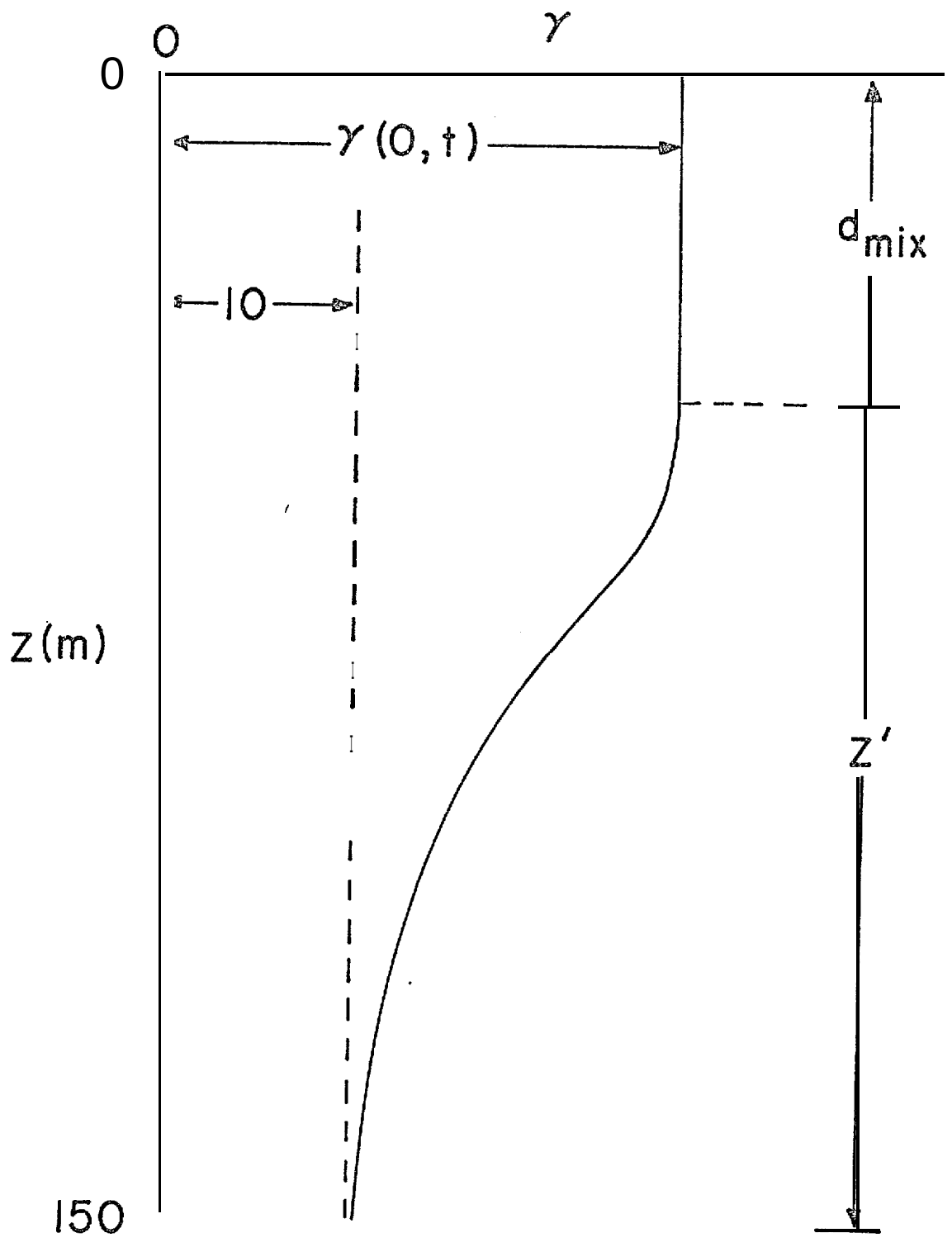


Figure 12. Depth dependence of the carbon-to-chlorophyll ratio.

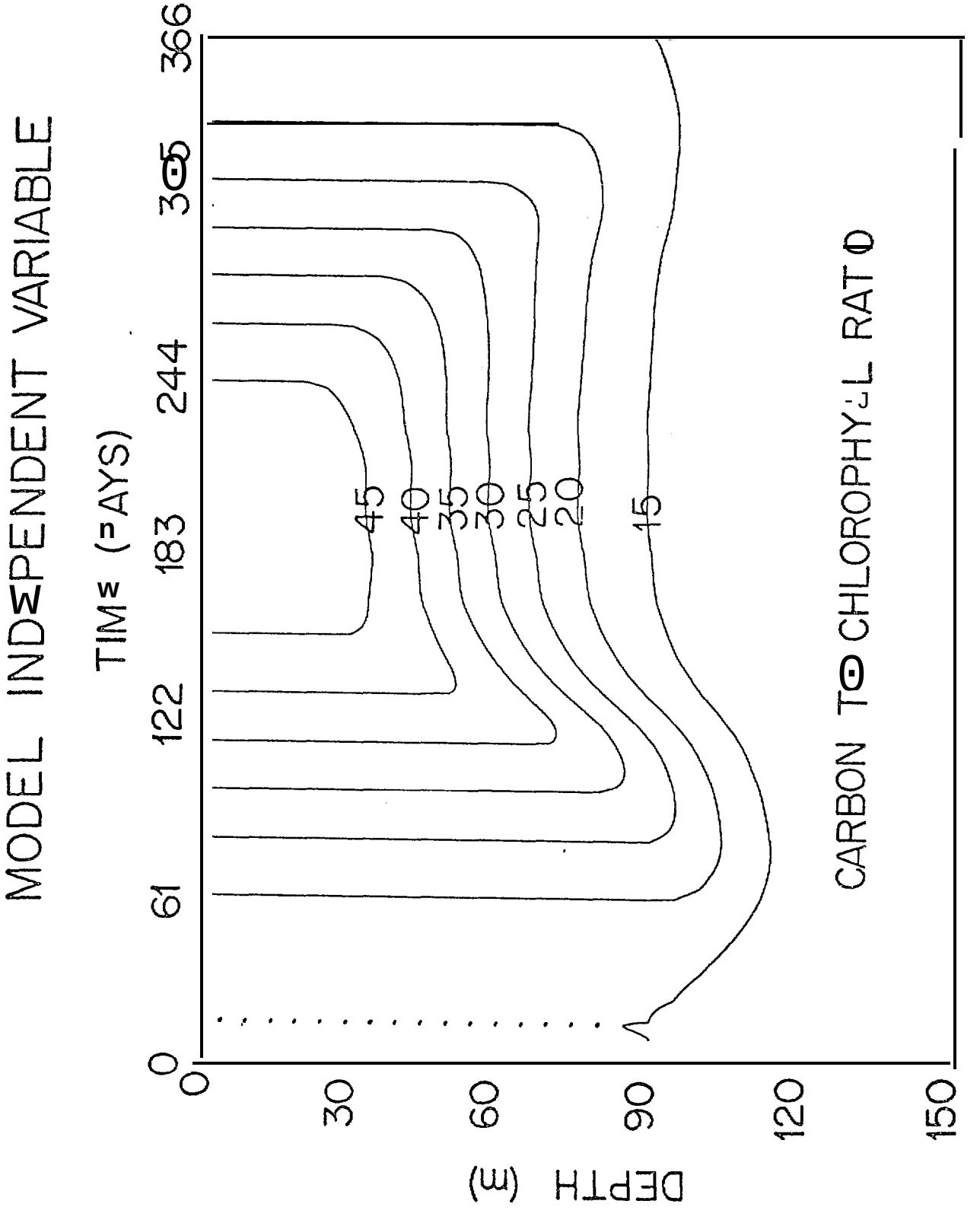


Figure 13. Carbon to chlorophyll values for one year.

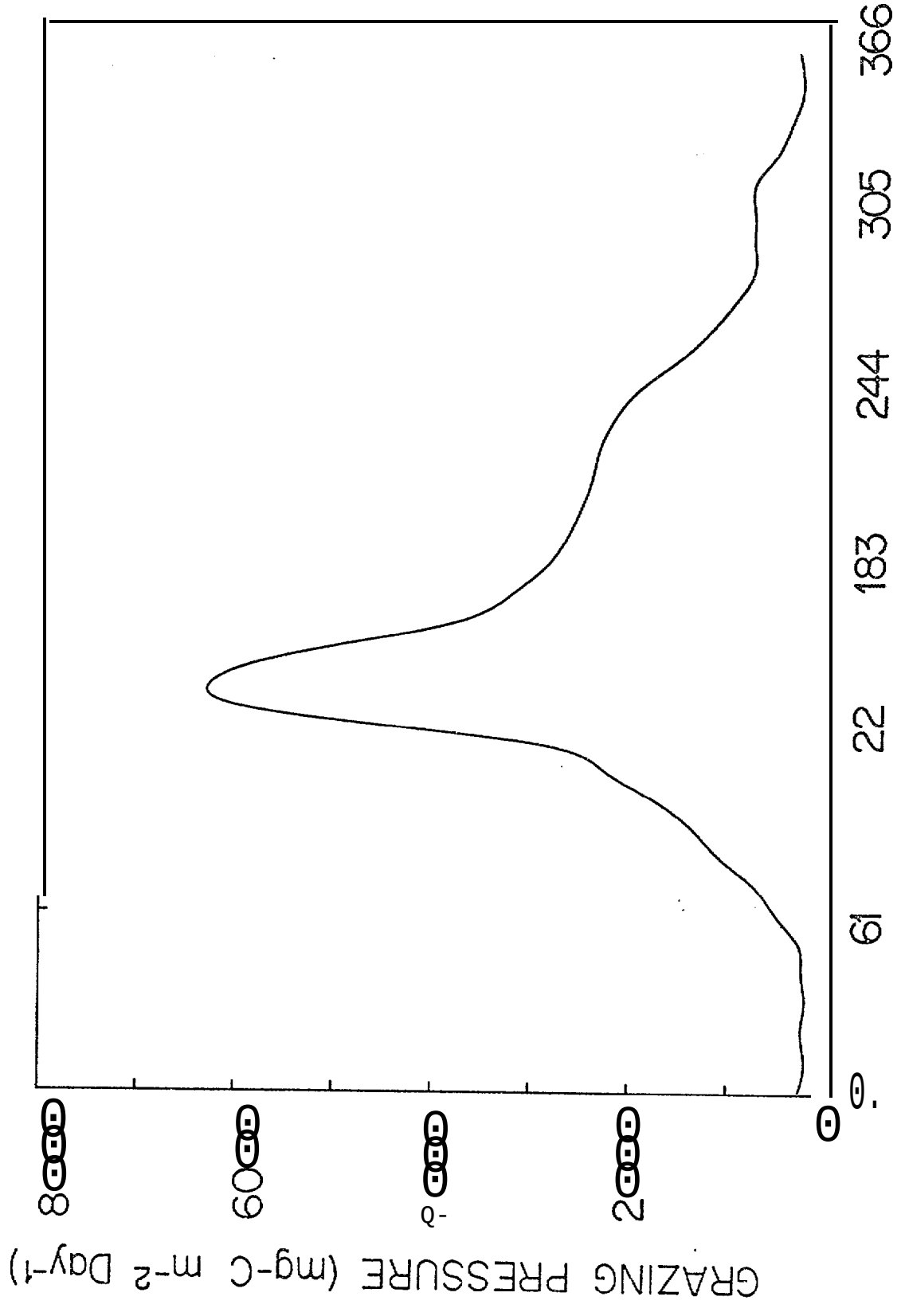


Figure 14. Seasonal variation in grazing pressure.

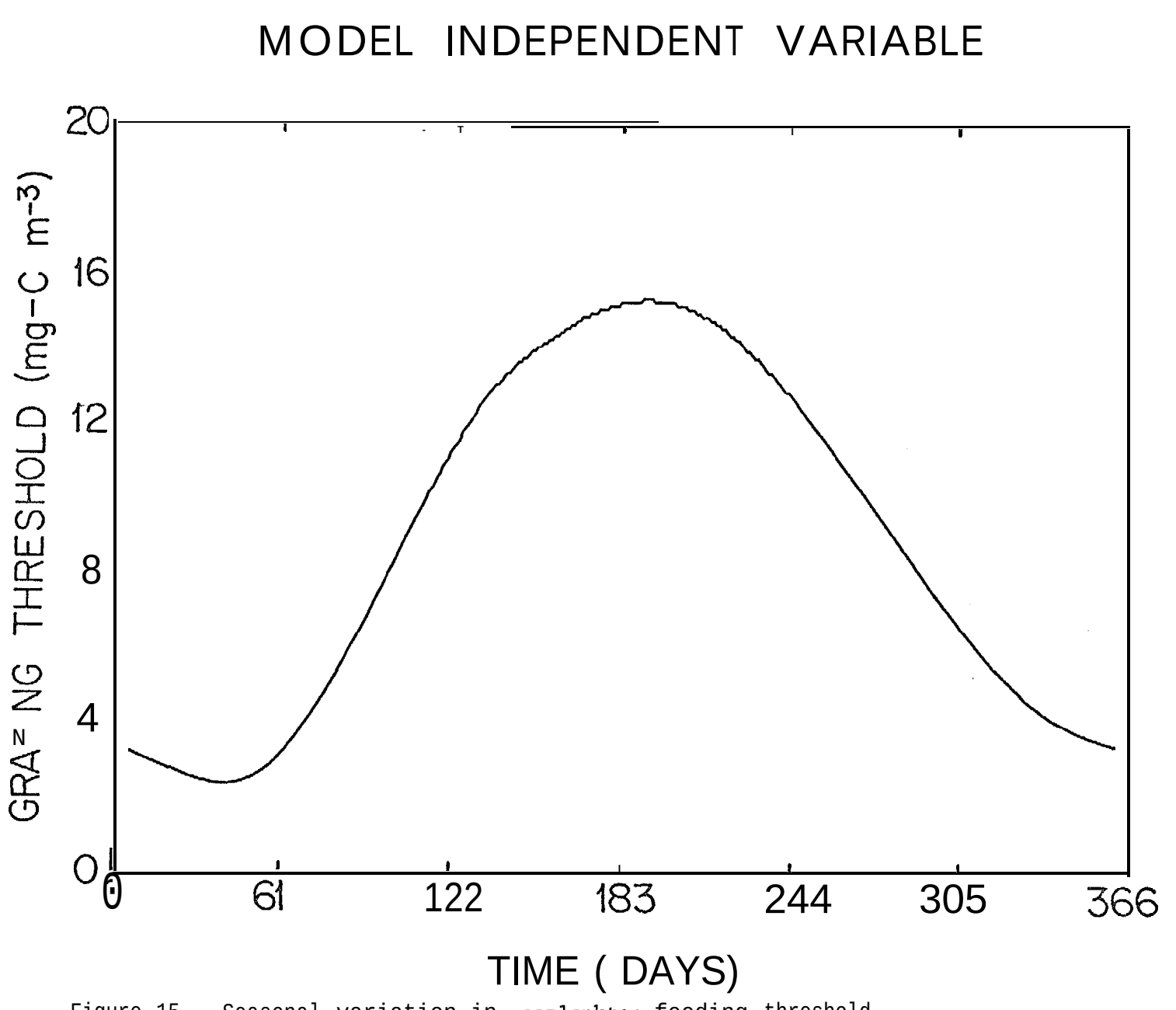


Figure 15. Seasonal variation in zooplankton feeding threshold.

minimum feeding threshold in the winter and a maximum threshold in the summer is consistent with the idea that the threshold increases with increasing animal size (Lam and Frost, 1976) and with the expected seasonal variations in zooplankton size distribution.

Constants in the standard run

As mentioned previously, nine physical and physiological constants must be specified in the model. These include w , the sinking speed of the algae; τ_s , c_1 , C_2 , and δ which affect the in situ light intensity; terms in the description of net production, P_{max} , α , and R; and β which occurs in the description of grazing.

A constant value of w = 0.5 m day^{-1} was chosen for the sinking speed. This is the sinking speed for an actively growing unicellular alga in the 10-20 μ size range (Smayda, 1970).

An atmospheric transmission coefficient, $\tau_s = 0.95$ and a sea surface penetration fraction of 0.85 (Parsons and Takahashi, 1973) were chosen for the model. Self shading by the plants results in $c_2 = 0.14$ $m^2(mg\text{-}chl)^{-1}$ (Lorenzen, 1972) and a value of $c_1 = .071$ m^{-1} was taken so as to place the 1% light level at a depth of approximately 60 m (Lorenzen, personal communication). In the model, we assumed that only one half of the measured radiation contributes to photosynthesis (Strickland, 1958).

Values for P_{max} and α were based on production rate data obtained near Station "P" and on considerations of the temperature-dependence of P_{max} (Eppley, 1972). These data included two cruises taken by the University of Washington in 1971 and 1973 and data taken near Station "P" in 1969 (Takahashi,

et al., 1972). The P vs I curves reported for 1969 were from 3-4 hour incubations with daylight fluorescent lamps using the C^{14} method. Photosynthesis was given as mg-C (mg-chl hr)$^{-1}$ and light intensity was reported in Klux. The light" intensities for the different data sets were converted to ly hr^{-1} using conversion factors given by Strickland (1958) for photosynthetically active radiation. These factors are:

$$1 \text{ ly hr}^{-1} = 2.8 \text{ Klux}$$

$$= 0.25 \text{ K foot candles}$$

The values for the initial slope ranged from a high of 2.8 to a low of 0.44 with a mean of 1.55 and an adjusted standard error of 0.25. The data give maximum production rates as carbon produced per unit chlorophyll whereas P_{max} is the specific production rate. It was necessary, therefore, to multiply the maximum production rates found in this data by the carbon-to-chlorophyll ratio, γ, in order to obtain P_{max}. γ, however, was not reported for the productivity experiments so we used the γ values from Figure 13. Resulting P_{max} values range from 0.02 to 0.22 and have a mean of 0.09 and an adjusted standard error of 0.02. The values of P_{max}, α, and the assumed C:chl values for the data are summarized in Table 2. A value of $\alpha = 1.6$, the mean data value, is chosen for the standard run. This is consistent with the range of α from 1.12 to 1.68, reported by Steemann-Nielsen and Jorgensen (1968). Eppley (1972) showed that laboratory cultures of algae grown under continuous light have:

$$P_{max} = .851 \times 10^{0.0275T}$$

where T is the temperature in "C and P_{max} is given in doublings per day. Thus, for T = 5°C, $P_{max} = 0.049$ and for T = 11°C, $P_{max} = 0.071$ An average of these two values, $P_{max} = 0.06$, was chosen for the standard run. This value is lower than the average P_{max} from the data but still within the range of P_{max} values "measured" at Station P.

Table 2.

Identifier	Depth (m)	P_{max} (hr^{-1})	α $\frac{mg\ C}{mg\ Chl\text{-}ly}$	Assumed C/Chl	Date
TT059 Sta. 51	3	---	.67	47	6/71
	15	.09	.79	47	"
TT082 Sta. 35	0	.14	2.0	49	8/73
	30	.08	2.0	49	"
Sta. 36	0	.22	2.3	49	"
	20	.22	2.3	49	"
Sta. 37	10	.02	.47	49	"
	50	.03	.47	35	"
Sta. 38	10	.07	2.8	49	"
	75	.06	2.8	22	"
Sta. 41	10	.14	2.5	49	"
	75	.11	2.5	22	"
Takahashi, et al. (1972)	10	.04	.72	46	8/69
	40	.03	.44	40	"
	70	.04	.44	25	"
Average		.09	1.55		
σ		.07	.98		
$\sigma/\sqrt{n}$		.02	.25		

Respiration rate, R , was taken as 0.07 x P_{max} (i.e., R= O.0042) for the model runs. Steemann Nielsen and Jorgensen (1968) state that respiration rate is 5 to 10% of light saturated photosynthesis, while Tailing (1960) gives a value for respiration of 5 to 20% of maximum photosynthetic rate. In reality, respiration rate, like photosynthesis, is temperature dependent (Riley, Stommel & Bumpus, 1949) where the specific respiration rate per day is given by:

$$R = 0.0175\ e^{0.069T} \qquad (15)$$

It is consistent with our choise of an average, constant value for P_{max} that the respiration rate is also taken to be a constant. The value chosen is close to the lower limit of that suggested by Steemann Nielsen & Jorgensen as well as Tailing but is considerably larger than the value suggested by Equation 15.

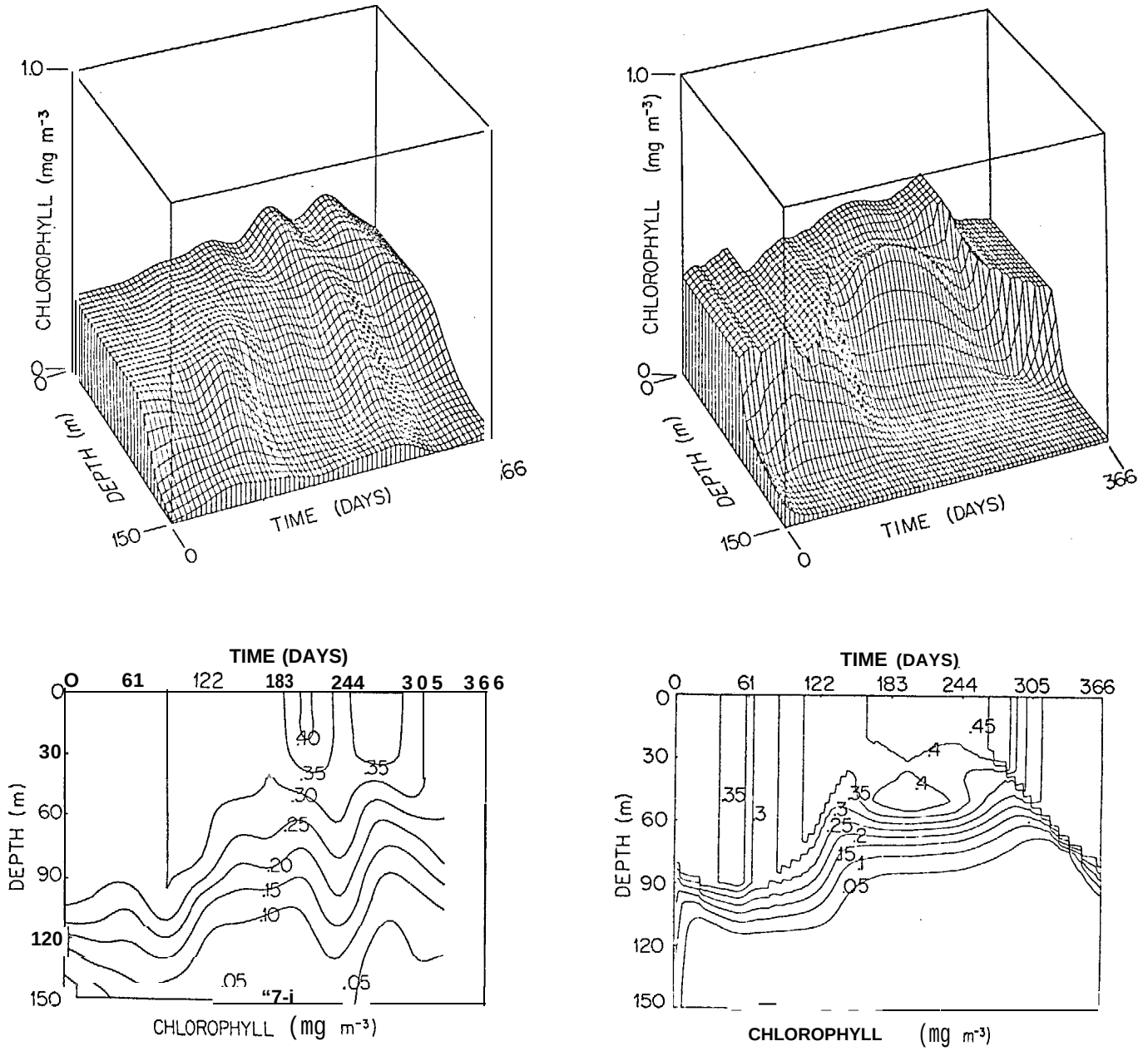
Method of solution

The Crank-Nicholson method was used to solve the production equation (Jamart, *et* aZ., in press). Time steps of one half hour and five meter depth intervals were used in all of the numerical simulations.

E. Model results

Standard run

Using the independent variables and constants which were just presented, the model was started *on* the first day of the year with an intial chlorophyll profile and allowed to run for one full year. The evolution of the chlorophyll concentration through time is presented in Figure 16b. Observed chlorophyll data (Figure 3) is reproduced in Figure 16a for comparison. General features such *as* the seasonal variation in the depth of the uniform, near-surface concentrations and the maximum standing stock in late summer compare well. Differences in the details like the double surface



(a) (b)

Figure 16. Comparison of modeled chlorophyll concentration (b) with average concentration data from Figure 3 (a).

chlorophyll peaks in the data or the spring chlorophyll minimum in the model are to be expected. We find from the large standard deviation in the chlorophyll data (Figure 2) that the observed double peak is not statistically significant. Likewise, details of the modeled chlorophyll concentrations are influenced by misrepresentations of the independent variables. Since the model run used averaged data to generate the independent variables and since these averages were often for different time periods, we should not place much emphasis on the smaller details of the model.

Figure 17 compares the modeled chlorophyll concentrations in the mixed layer with the data for the surface chlorophyll. From this comparison, because of the large scatter in the data, we can only say that the model results are not inconsistent with the measurements. The integrated values for net production from the model are plotted, along with the observed values, in Figure 18. Both the model and the data show a peak in production at the beginning of the summer.

Sensitivity analysis

While creating the standard run, we found that the relative importance of the different inputs and coefficients on the chlorophyll distribution changes with time. We also discovered that, in the mixed layer, turbulent mixing and algal sinking were relatively unimportant when compared with net production and zooplankton grazing. In this case, for the mixed layer, the production equation (equation 4) may be approximated by:

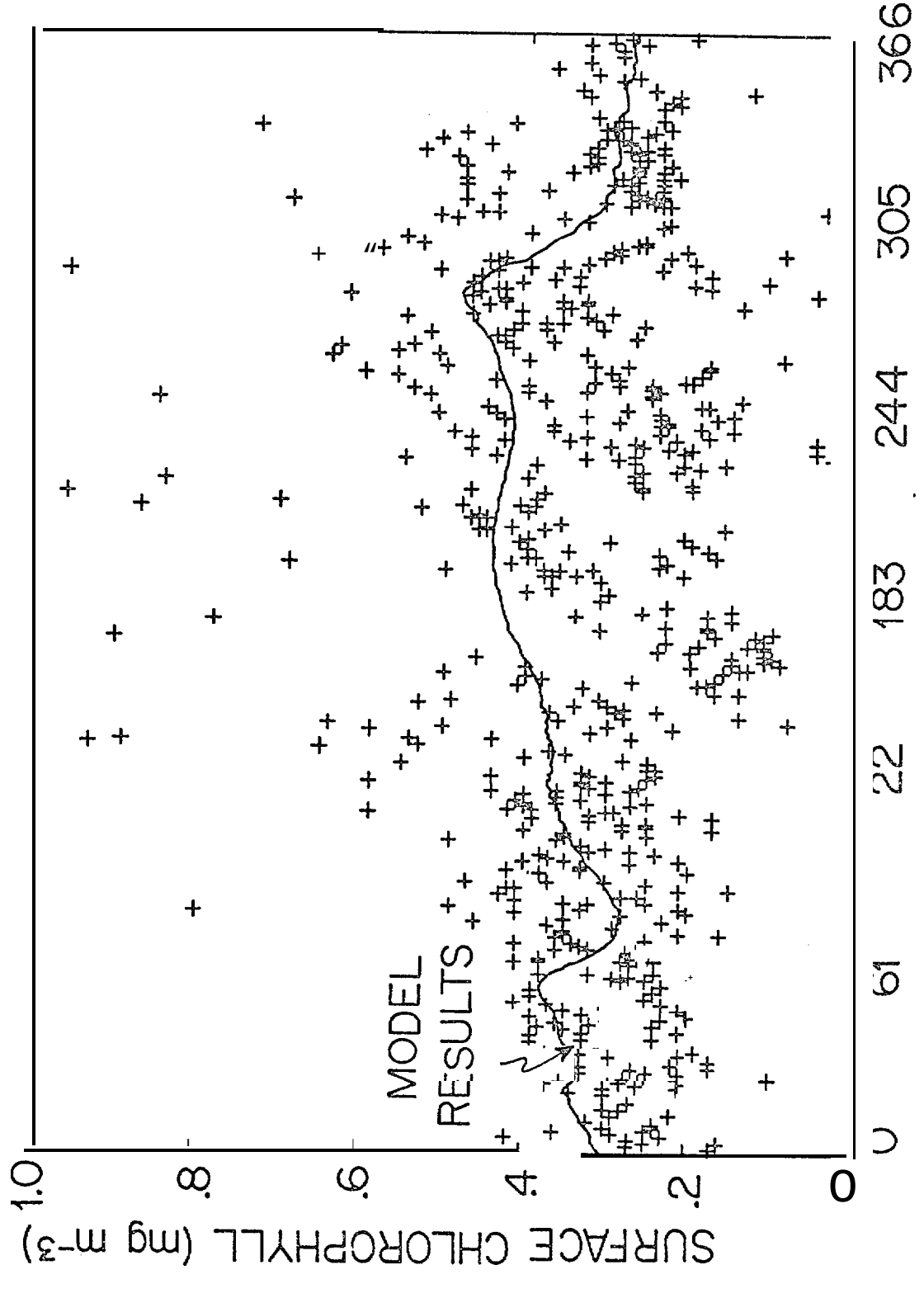


Figure 17. Comparison of modeled, mixed-layer chlorophyll with surface chlorophyll data from Figure 1.

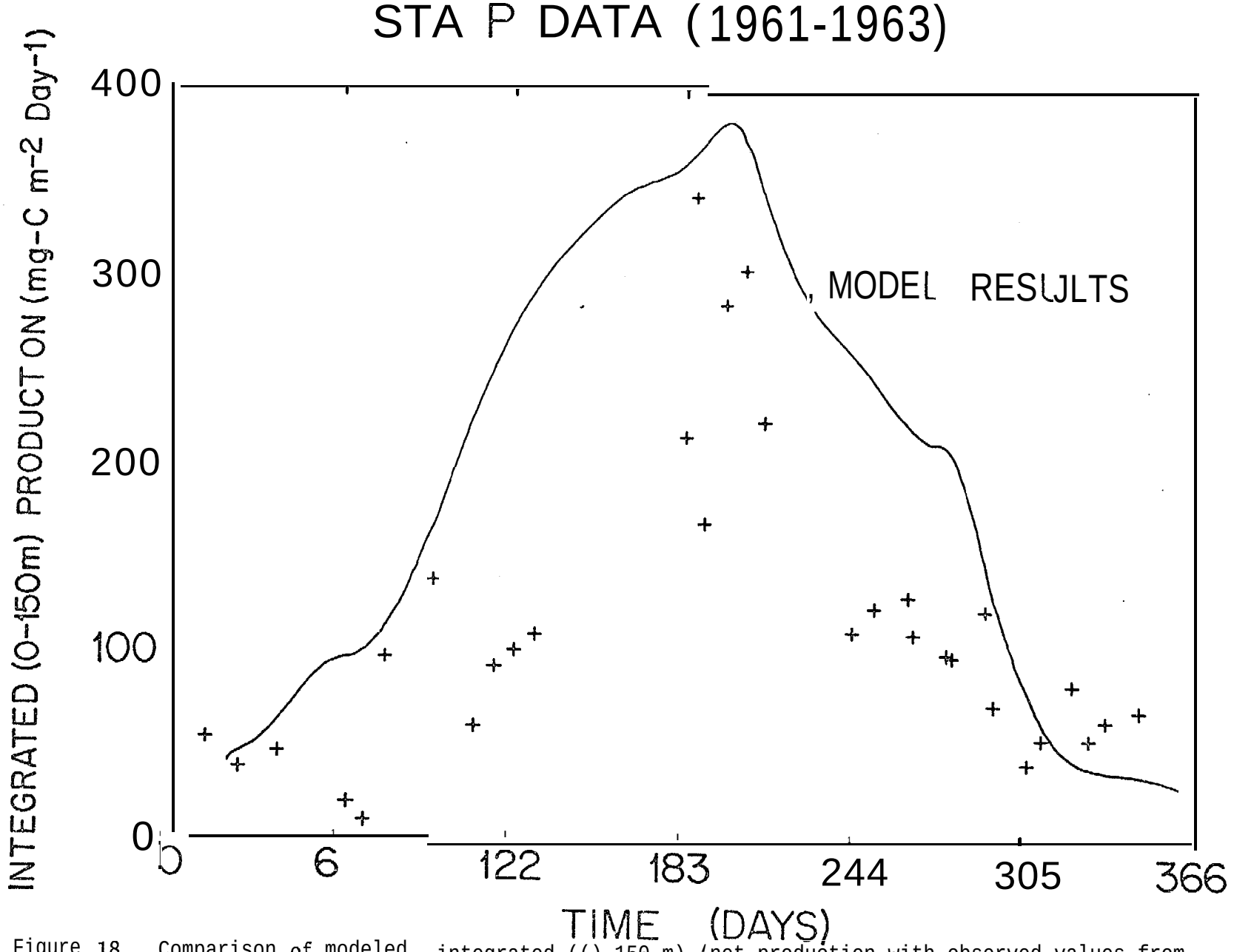


Figure 18. Comparison of modeled, integrated (()-150 m) 'net production with observed values from Figure 6.

$$\partial_t A = \left[P_{max.} \tanh\left(\frac{I\alpha}{P_{max}\,\gamma}\right) - R\right] A - \frac{G}{\gamma}\left[1-e^{-\beta(A\gamma-P_0)}\right]_{-1} \qquad (16)$$

At any given time, the independent variables and the constants may be specified so that equation 16 may be further simplified to:

$$\partial_t A = Q_1 A - Q_2\left(1-e^{-\beta(A\gamma-P_0)}\right); \quad A\gamma > P_0$$

$$= Q_1 A \qquad ; \quad A\gamma \leq P_0 \qquad (17)$$

Here Q_1 represents the net production rate and Q_2 represents the grazing pressure. In figures 19 and 20, we plot equation 17, showing the time rate of change in chlorophyll concentration against the chlorophyll concentration for various times of the year. For low chlorophyll concentrations ($A \leq P_0/\gamma$), the rate of change is proportional to the concentration. At higher values, the change is due to both a linear term and a grazing loss. For very high concentrations, the grazing loss approaches its asymptotic limit and we have:

$$\partial_t A = Q_1 A - Q_2 \qquad ; \quad A \to \infty$$

At each time of the year, the coefficients, Q_1 and Q_2, are calculated from the known independent variables and coefficients and from the average net production over 24 hours. Most of the rate curves in Figures 19 and 20 show increasing chlorophyll concentrations for both very high and very low chlorophyll concentrations and decreasing concentrations for the values in between. In these cases, there are two points where the rate of change in

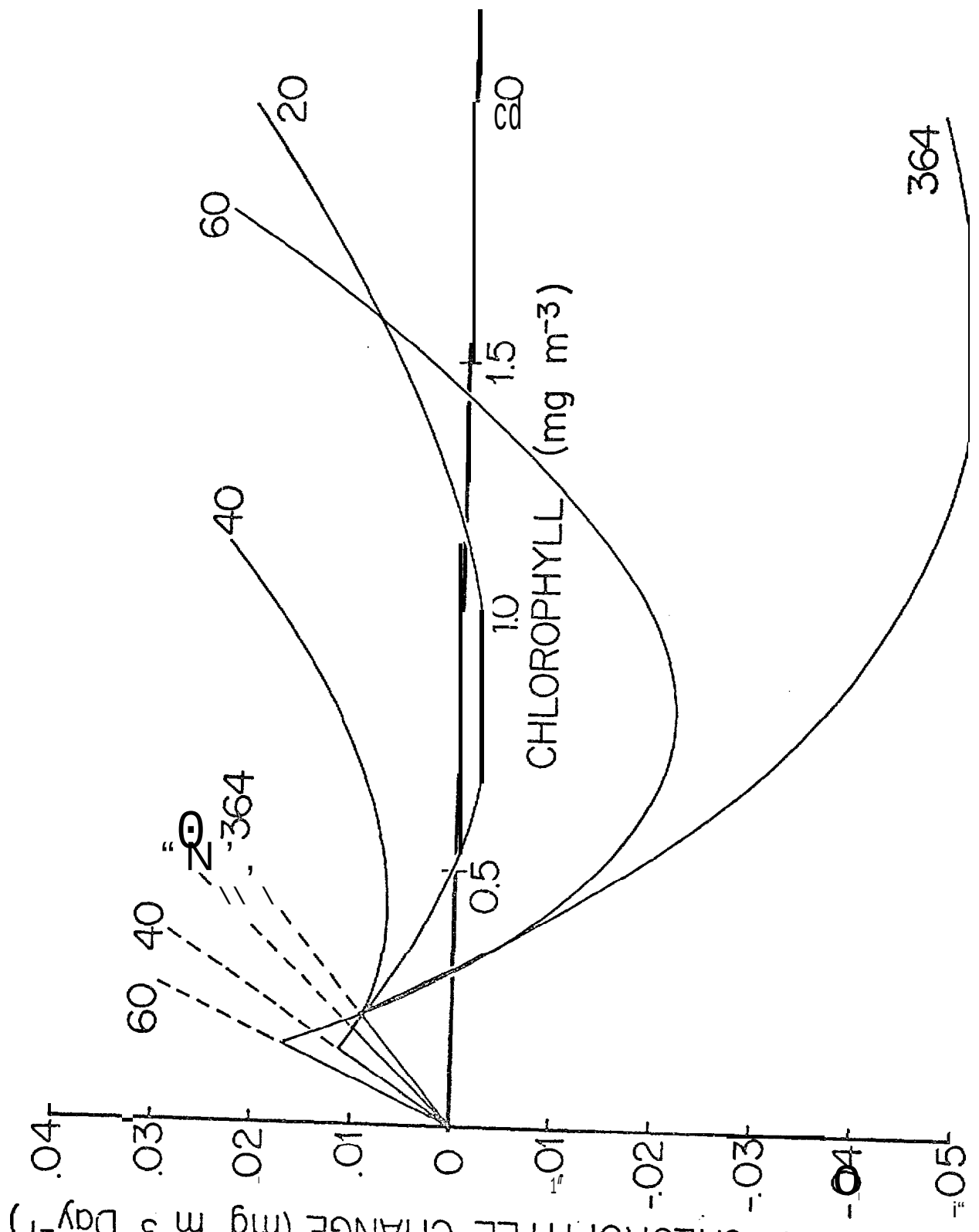


Figure 19. Plot of rate of change in the mixed layer chlorophyll concentration versus the chlorophyll concentration for days 20, 40, 60, and 364.

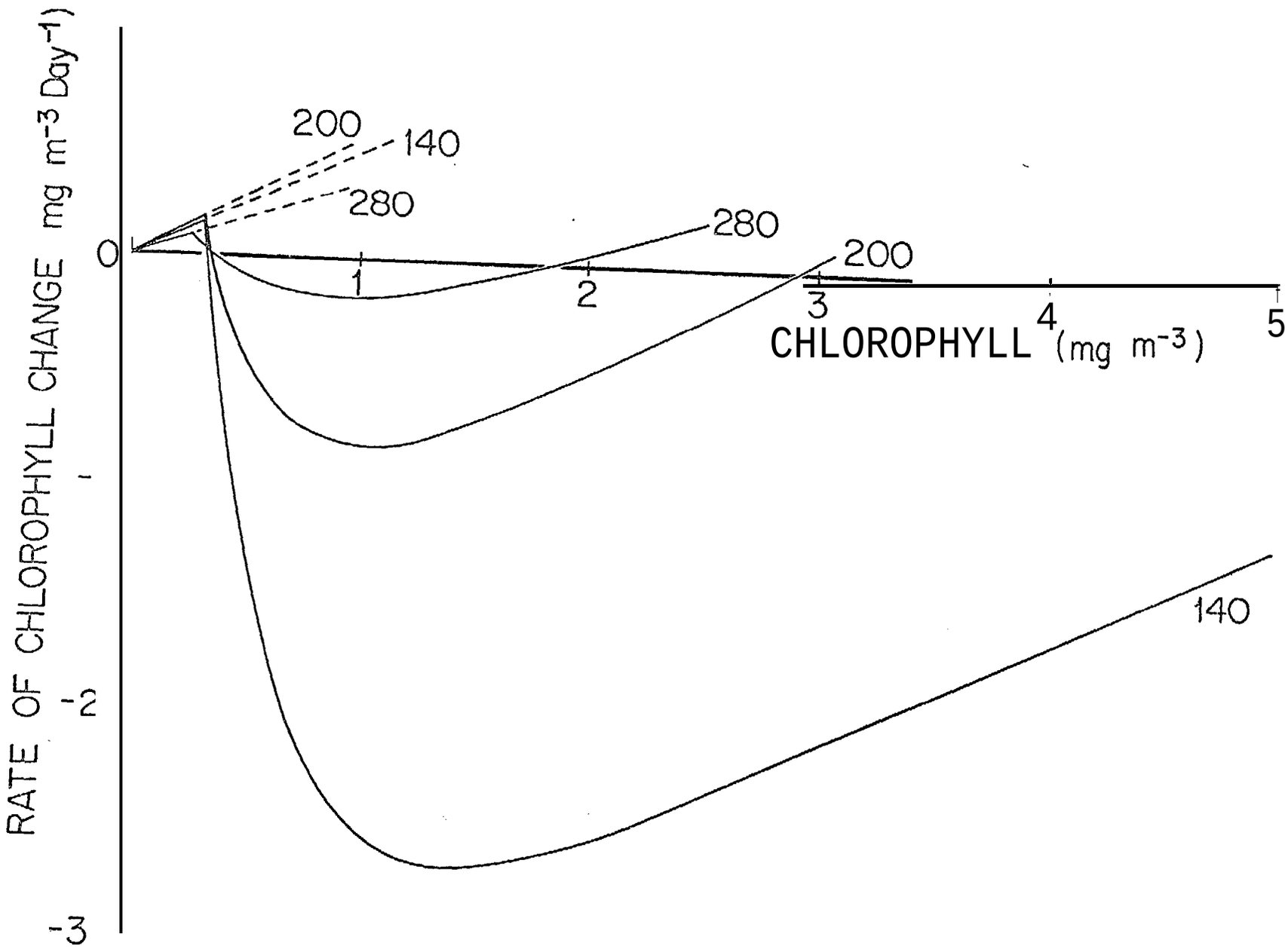


Figure 20. Plot of rate of change in the mixed layer chlorophyll concentration versus the chlorophyll concentration for days 140, 200, and 280.

plant material is zero, the zero crossings of the curve. For chlorophyll concentrations below the higher zero crossings, the biological system is stable and the chlorophyll concentrations will evolve toward the value at the smaller zero crossing. If concentrations had started out below this value, the rate of change would be positive and the chlorophyll concentrations would increase until the rate of change became zero. Likewise, if the plant concentrations were between the two zero crossings, the rate of change would be negative and the concentrations would decrease until the rate of change reached zero.

In this model, there are some situations which could cause the chlorophyll concentration to either grow unchecked or to approach zero. If chlorophyll concentrations are above the higher zero crossing, they will continue to increase with time at an ever accelerating rate. Another case where the plants might grow unchecked is illustrated by the case for day 40 in Figure 19. There, the combination of net production and grazing loss is such that the zooplankton can never keep the plants cropped down and the chlorophyll production rate is always positive. If net production, Q_1, were negative, possibly caused by an extremely deep mixed layer, the rate of change in chlorophyll content would always be negative so that the plants would disappear from the water column. In nature, unchecked plant growth is impossible and complete depletion of plant material is unlikely. In the" model, these two extreme cases either violate the assumptions or are poorly approximated by the model. In the first case, as the plant concentrations become very large, nutrients would certainly be depleted to the point where there would be nutrient limitation to growth. On the other hand, if conditions are unfavorable and net production becomes negative, plant respiration often decreases. This is not simulated in the model.

We see in Figures 19 and 20 that days 20 and 140 represent the cases where there are barely enough zooplankters to keep plant production in control and where there is a superabundance of zooplankters. These two time periods were chosen for sensitivity studies because they represent extreme cases. Equilibrium chlorophyll concentrations ($a_t A^{=} O$) were found for each of these periods by iteration from equation 17. Some of the inputs were then increased and decreased by 10% and new equilibrium values calculated. Table 3 lists the inputs which were changed along with the percentage change in the equilibrium chlorophyll concentrations for each of the two time periods. For day 20 in the early winter, the chlorophyll values changed by at least 10% in response to changes of any of the inputs. In many cases, a 10% change in inputs caused an imbalance between net production and grazing such that the chlorophyll values increased continuously and no equilibrium value was reached. In contrast, the equilibrium chlorophyll concentration on day 140 showed very little response to changes in the variables other than the feeding threshold and the carbon-to-chlorophyll ratio. The equilibrium concentrations changed by about 10% when those two inputs were altered. The response of the chlorophyll concentration to changes in the inputs should fall somewhere between these two extremes during the rest of the year.

The results which are summarized in Table 3 were verified by doing the same experiments on the computer model. Changing the inputs caused changes in the mixed layer chlorophyll concentrations which were very close to those predicted by Table 3.

Table 3. Percent change in equilibrium chlorophyll concentration (f r o m standard run) as the inputs are changed by ± 10%.

Day 20

Y	P_0	β	Q_2	Q_1	A
10					-25
-lo					*
	10				15
	-lo				-13
		10			-17
		-10			*
			10		-18
			-lo		k
				10	*
				-10	-19

* No equilibrium ($\partial_t A > 0$)

Day 140

Y "	P_0	β	Q_2	Q_1	A
10					-9
-lo					12
	10				10
	-lo				-lo
		10			- 0.3
		-lo			0.6
			10		- 0.3
			-lo		0.6
				10	0.6
				-lo	- 0.6

Simulated response to an oil spill

In this section, we show how the model might be used to simulate the effects of an oil spill on the standing stock of chlorophyll. Oil pollution has been postulated to cause a 50% reduction in the growth rate of marine phytoplankton at oil concentrations greater than 10 ppm (Mills and Ray 1977, Vaughn 1973, Kauss *et al.*, 1973, Strand *et al.*, 1971) and a 25% increase in growth rate at oil concentrations of 30 to 100 ppb (Prouse *et al.*, 1976, Gordon and Prouse 1973). Oil pollution is also likely to inhibit zooplankton feeding rates. The feeding rate of lobster larvae was reduced at oil concentrations greater than 1 ppm (Ferns 1977). Lobster feeding was reduced in the presence of a 10 ppm crude oil emulsion (Atemaand Stein 1974). Locomotory inhibition of an arctic amphipod occurred at oil concentrations of 400 ppm (Percy 1977). Prouse *et al.* (1976) found 16-41 ppb oil in the water column 3 months after the Arrow spill.

Guided by the above literature, we performed three sets of simulation experiments. In the first one, P_{max} was increased by 25%, decreased by 25%, and decreased by 50% in order to simulate the effects of increasing amounts of pollution. In the second set, grazing pressure was decreased by 10%, 25%, and 50%. Finally, both P_{max} and the grazing pressure were reduced by 50% to simulate the combined response of the biological system. In all cases, the model was run for two 60-day periods, days 20 to 80 and days 120 to 180. These two periods were chosen to include the times of low and high zooplankton pressure, the ones which were examined in the sensitivity analysis. Each simulation run started with the chlorophyll distribution from the appropriate day of the standard run. Then P_{max} and/or the grazing pressure was changed

and the model was allowed to run for 60 days with all other inputs unchanged.

In Figure 21, the mixed layer chlorophyll concentrations from the standard run and from the simulation runs where P_{max} was changed are shown together. As expected, the concentrations increased when P_{max} was increased and decreased when it was lowered. Changes in chlorophyll standing stock changed more during the first period of the year than in the second in response to changes in P_{max}. This too is consistent with the results of our sensitivity analysis. During the period beginning with day 20, the perturbed concentration values first diverged from those of the standard run but then converged towards them again towards the end of the 60 days.

Figure 22, illustrates the case where grazing pressure is reduced. When that pressure is reduced by 10% or 25%, the results are qualitatively similar to those of Figure 21: changes during the second period are less than those of the first and the perturbed values during the first period diverge from and then reconverge towards the standard values. When grazing pressure is halved, chlorophyll blooms occur for both time periods. In the second period, however, that bloom does not begin immediately and is only initiated (sometime after day 140) when the grazing pressure has dropped. Further computer simulations showed that even when grazing was reduced 50%, the blooms did not go unchecked and chlorophyll values did decrease at some later time.

Finally, Figure 23 illustrates the combined effects of decreasing both P_{max} and grazing pressure by 50%.

These three simulation exercises are only meant to illustrate one possible use of a model; the results must be interpreted with great caution. For instance:

- The results illustrate only the effects on plant biomass and do not address questions concerning long-term, low-level effects or influences on other trophic levels.

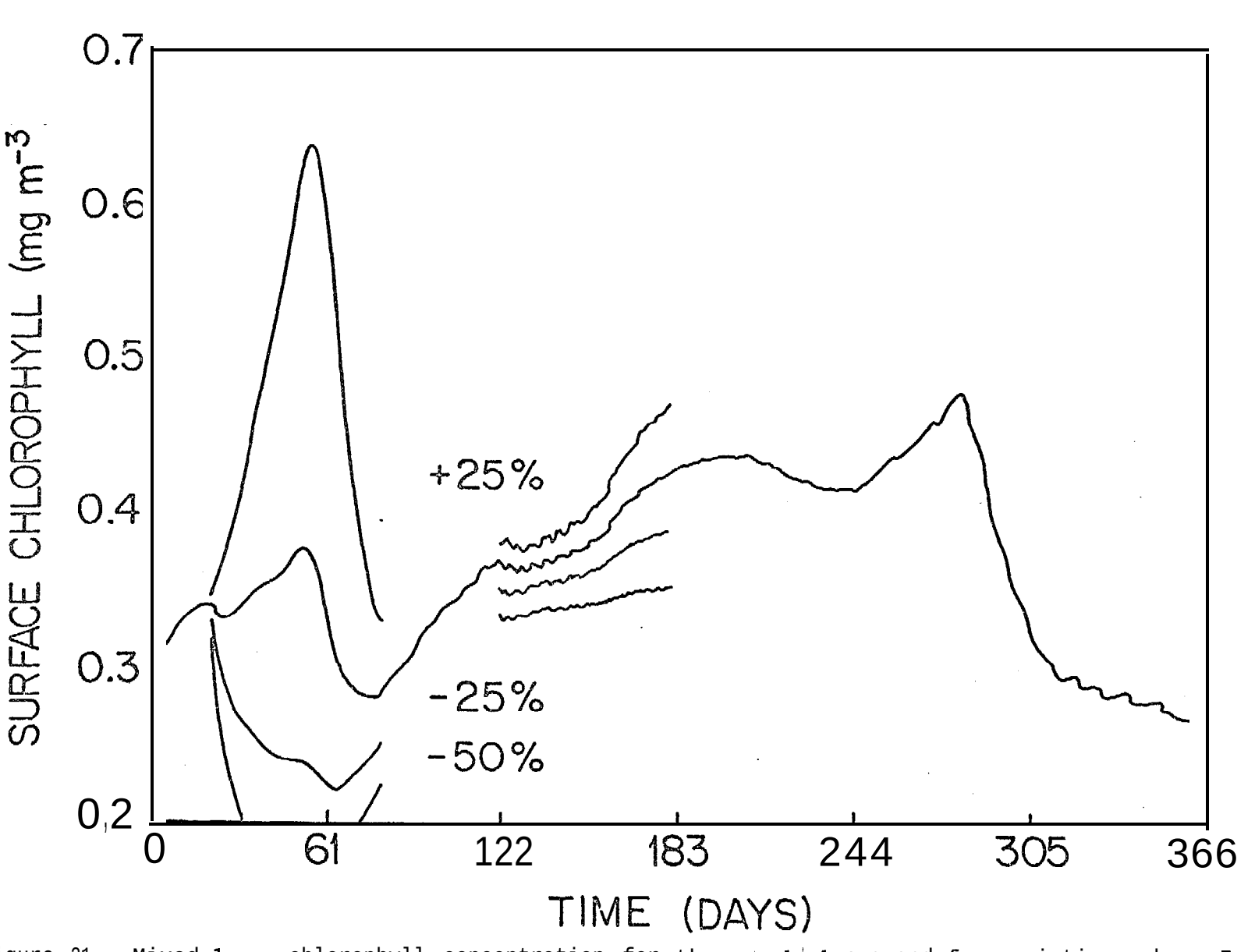


Figure 21. Mixed layer chlorophyll concentration for the standard run and for variations where P_{max} is changed, as indicated. The variations are run from days 20-80, and days 120-180.

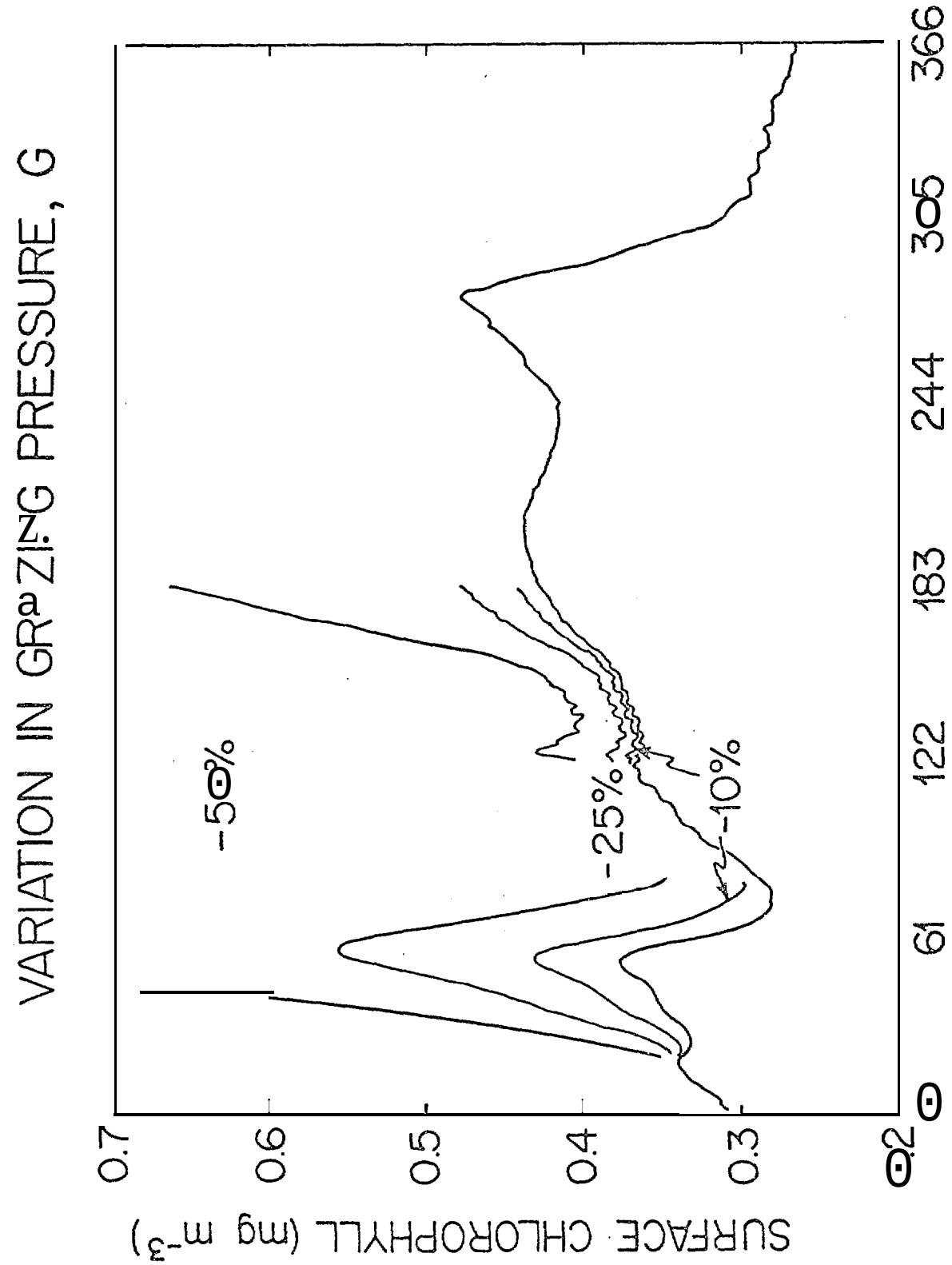


Figure 22. Mixed layer chlorophyll concentration for the standard run and for variations where grazing pressure is changed, as indicated. The variations are run from days 20-80 and days 120-180.

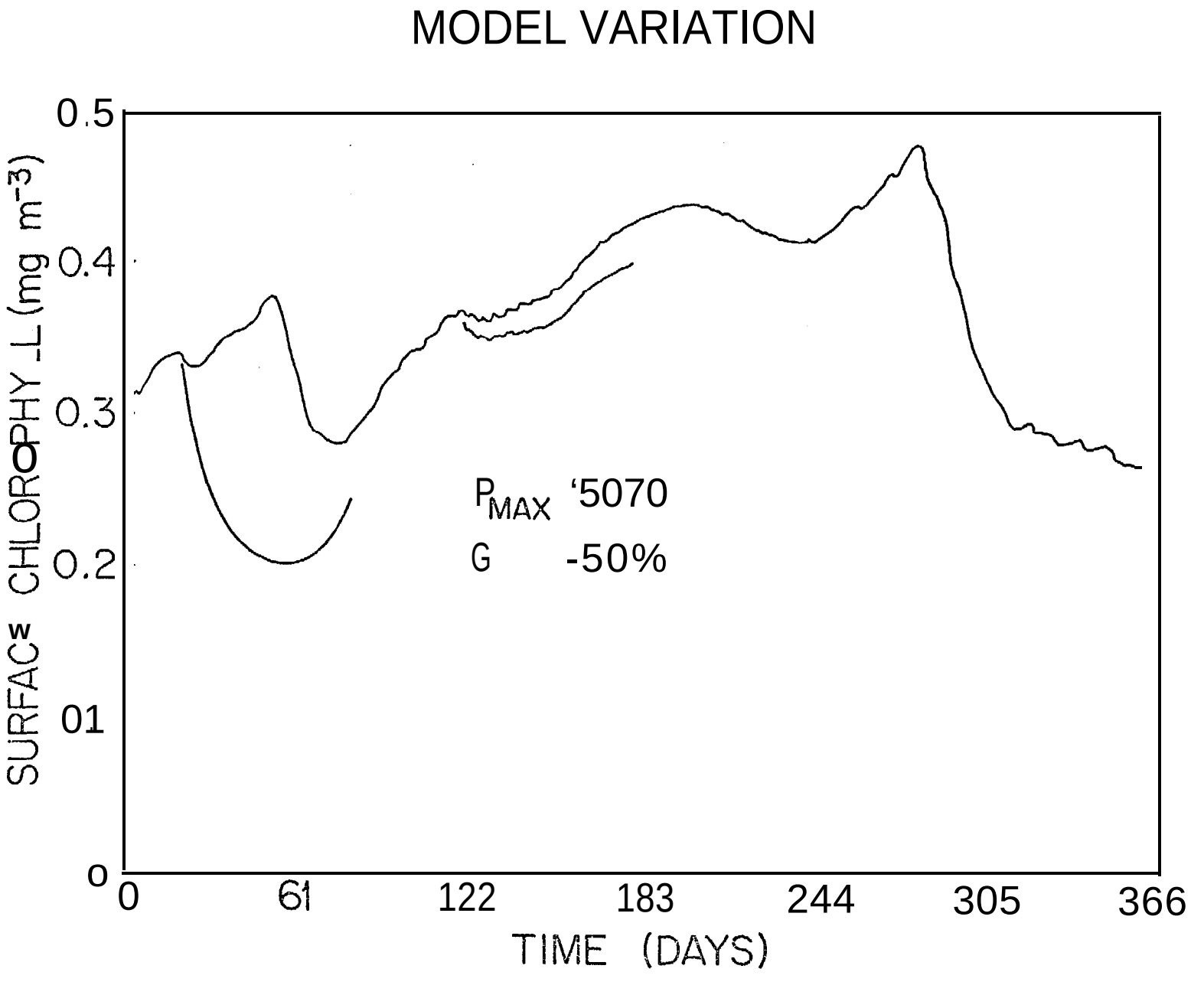


Figure 23. Mixed layer chlorophyll concentration for the standard run and for variations where P_{max} and grazing pressure are changed, as indicated. 'She variations are run from days 20-80 and days 120-180.

- Effects of oil on other than P_{max} and the grazing pressure have not been considered.
- A different model (different standard run) might produce very dissimilar results.

F. Summary and conclusions

We have synthesized a relatively uncomplicated model of primary productivity at Station "P". When we apply biologically and physically reasonable inputs to this model, the results are in agreement with observations for that location. The model is more sensitive to change in the inputs during the winter months when zooplankton biomass is 10-w than during the spring time with greater zooplankton grazing pressure. Whereas the results were sensitive to net production, zooplankton biomass, carbon-to-chlorophyll ratio, and the feeding threshold during the winter, the model was only sensitive to the last two variables during the high biomass period. Unfortunately, both the time variation in the feeding threshold and the time-depth structure of the carbon-to-chlorophyll ratio are very poorly known. Because of this and since there is a wide latitude in the choice of many of the other inputs, we can only assert that this is one model which is applicable to Station "P". Other combinations of processes and inputs may also be able to explain the data.

There are reasons to include two equations to describe the time rate of change in zooplankters and in nutrients in future work. Including a zooplankton equation may very well degrade the results and introduce more uncertainties. However, that would be more useful in simulating a perturbed system since the plants and animals do interact and change together. When we perturb the system now, we allow the chlorophyll content to change but

do not allow the zooplankton biomass to adjust accordingly. Since nutrients do not appear to be limiting, introducing a nutrient equation should not alter the results of the standard run. However, it would provide a description of nutrient concentrations which could be compared to the data, for another check on the model. Also, a model which includes nutrients would be more applicable for those perturbations which now cause large phytoplankton blooms.

BASELINE DATA

A. Current state of knowledge

The first studies of the lower trophic levels of the eastern Subarctic ecosystem (Holmes, 1958; McAllister *et al.*, 1960; Parsons, 1965) were limited by a small data base. The" data base has been expanded both geographically and temporally over the last twelve years.

Some of the readily available information on the physical oceanography of the Subarctic Pacific Ocean has been described by a number of authors (e.g., Tully and Barber, 1960; Uda, 1963; Dodimead, Favorite and Hirano, 1963; Tully, 1964 ; Tabata, 1965; and references cited therein). Similarly, some of the major publications of biological data for the same area include the works of McAllister, Parsons and Strickland, 1960; Anderson, Parsons and Stephens, 1969; Parsons and LeBrasseur, 1969; Parsons and Anderson, 1970; Larrance, 1971a; and Anderson and Munson, 1972. Other relevant biological information from the area are contained in the north-south sections made through the Gulf in past years, e.g., Ursa Major and Zetes expeditions in 1964 and 1965 (University of California, 1967, 1970), the HAKUKŌ MARU in 1969 (Marumo, 1970), and the R/V T.G. THOMPSON in 1972. Also, a winter cruise in February 1967 by the R/V THOMPSON covering a large area of the Gulf of Alaska has produced a unique set of data on primary production, plant nutrients, and hydrography at *a* time when observations are most difficult to obtain.

One of the largest blocks of existing data was obtained through several decades of study carried out by Canadian oceanographers at Ocean Weather Station "P", the results of which are reported in various papers and technical reports. A second very large block of data was obtained during a five-year

study (January-June, 1968-1972) made from commercial vessels crossing from North America to Japan via the Gulf of Alaska and near to the Aleutian Islands (Anderson and Munson, 1972; Munson, in preparation). In these Ships of Opportunity studies, enumeration of phytoplankton species and measurements of surface chlorophyll and nutrient concentrations, productivity, zooplankton volume, depth of mixed layer, temperature, and insolation were made at frequent intervals during the period of the spring bloom. In addition to the measurements made from the commercial vessels, more sophisticated sampling from research vessels including measurements of the vertical distribution of parameters was carried out from a number of oceanographic cruises taken over similar cruise tracks. In March and April 1969, studies were conducted by the Fisheries Research Board of Canada, Nanaimo (T. R. Parsons] aboard the ENDEAVOUR (Anon, 1970); in June and July 1970, samples were collected by Hokkaido University (S. Motoda) aboard the OSHORO MARU (Faculty of Fisheries, 1972) and the University of Washington (G. Anderson) made similar measurements from the T.G. THOMPSON in the spring of 1971. Other biological cruises aboard the R/V THOMPSON were made during the summers of 1973 and 1974.

Coastal areas which have received intensive investigation are the Aleutian chain (McAlister, 1971), the inland waters of Alaska (Bruce, 1969; Iverson *et al.*, 1974; Curl, 1972; Iverson, 1972; DeManche, 1974; Kirk, 1973; Schell, 1974; Iverson, Curl, and Saugen, 1974; Goering *et al.*, 1973; Homer *et al.*, 1973), and British Columbia (Parsons, 1965; Gilmartin, 1964; Parsons *et al.*, 1969, 1970; Strickland, 1959, 1961; Waldichuck, 1956; Stockner and Cliff, 1975, 1976; Takahashi et aZ., 1973). Some of the above data have been summarized *to* describe features of the distribution of biological parameters in the Northeast Pacific:

Seasonal variation

Evidence of seasonal variation has been derived from long-term monitoring at Station "P" (145°W50°N). In contrast to the marked phytoplankton blooms

over the Continental Shelf, phytoplankton biomass in the open ocean region of 145°W50°N remains relatively constant throughout the year. In this area primary production increases in the spring months, and grazing is assumed to keep the plant biomass constant (McAllister, *et* al., 1960) .

The investigations show that there are high nutrient concentrations in the waters of the Gulf of Alaska during the winter, and in the summer the nutrients in the coastal waters are substantially reduced while the nutrients in the oceanic waters, though reduced, remain in fairly high concentration. Nevertheless, surface concentrations of phytoplankton in oceanic waters remain quite uniform throughout the year. Parsons and LeBrasseur (1969) have hypothesized from the relationship between thermocline depth and incident radiation that the spring increase in primary production should begin in March around the edge of the Gulf of Alaska but not until May in the central portion of the Gulf. This shorter period of plant growth from the coast outward is offered as an explanation for the reduced level of nutrient removal from offshore oceanic waters as compared with coastal waters. It is further suggested (McAllister *et al.*, 1960) that secondary production in the offshore waters also contributes to limting the standing stock of phytoplankton during spring and to recycling nutrients. In the winter, high vertical mixing in combination with low light intensities result in higher nutrient concentrations in the surface waters.

Annual variation

Large-scale, non-seasonal fluctuations of biological parameters have been observed in the vicinity of Station "P". Intrusion of mixed Transition waters from 1958 to 1960 brought warmer temperatures with lower oxygen concentration than in Subarctic waters which normally occur there (Parsons and LeBrasseur, 1967; Marlow and Miller, 1975). The, presence of Transition waters at the surface produced biological differences in underlying waters (Geynrikh, 1968) . For example, while the zooplankter *Calanus pacificus* occurred in all

Subarctic waters, *Parathemisto japonica* was not found in Subarctic water overlain by Transition water (Beklemishev, 1969). From 1962 to 1964, zooplankton biomass at Station "P" decreased to one fifth its normal level (Longhurst, *et al.*, 1972). The decrease was not correlated with any other parameter, biological or physical. Other unexplained non-seasonal variations in salinity and oxygen content have also been observed at Station "P" (Marlow and Miller, 1975; Tabata, 1965). Intrusion of deep water below the halocline from the western into the eastern Subarctic Pacific has been documented for the years 1959 to 1965 (Favorite, person communication). The intrusion has not been correlated with any biological events above the halocline.

Geographic variation

Fewer studies have dealt with geographic variation of biological features in the eastern Subarctic Pacific. Venrick (1969) found the neritic phytoplankton to be markedly distinct from the oceanic species, and the boundary between oceanic and neritic to be very sharp. Larrance (1971a) found productivity and chlorophyll *a* substantially higher in coastal waters of the Aleutian chain than in the Alaskan Stream. Beklemishev and Nakonechnaya (1972) found discrete phytoplankton blooms in both Subarctic and Transition Zone waters. The smallest patches had dimensions of 150 x 420 nautical miles. The patches in the Subarctic water coincided with the area of high phytoplankton biomass described by Parsons and Anderson (1970).

Many of the problems encountered in studies of variation within large scale ecosystems have been discussed by Kerr and Neal (1976). They point out the difficulty of distinguishing patterns within a system containing excess "noise". They note that physical and chemical processes are ultimately responsible for biological variation but that the relationships 'are not direct and are therefore difficult to discern. One of the main problems of large scale ecosystem studies, therefore, is that the very process of organizing and grouping data for

descriptive analysis obscures many causative features and quantitative relationships.

In this paper we describe a large-scale ecosystem study of the eastern Subarctic Pacific using a variety of data from both published and unpublished sources. We adopt the idea put forward by Kerr and Neal (1976) that an ecosystem can be defined as a list of variables.

B. Study area

In order to obtain as much baseline data as possible, the study area covers the Gulf of Alaska expanded west to 180° and south to 42°N. This area includes the entire eastern Subarctic (excluding the Bering Sea) as well as part of the Transition Zone. For the numerical model, Weather Station "P" has been chosen as the study area because of the extensive time series of biological and physical data collected there.

c. Materials and methods

Data collection and adjustment

Source of data: Biological oceanographic data collected from the eastern Subarctic Pacific between 1958 and 1974 were compiled from published and unpublished sources (Table 4). The study area was bounded by the 180° meridian, the 42° N parallel, and the Alaskan, British Columbian, and Washington coasts. The major types of data collected on each cruise are listed in Table 4. To ensure comparability, only data from selected methods were compiled; and some systematic corrections which are described below were made. The data have been filed with National Oceanographic Data Center, Rockville, Maryland.* -

Chlorophyll a: Chlorophyll a concentration may be used as an index of phytoplankton standing stock. The laboratory technique for the spectrophotometric method has remained essentially the same since its development (Richards

* OCSEAP RU 58 Tapes #1 and #2.

Table 4. List of operations in the eastern subarctic Pacific between June 1958 and July 1974 which yielded biological oceanographic data.

[C = chlorophyll a/m^3, C' = chlorophyll a/m^2, Ph = phaeopigments/m^3, Ph' = phaeopigments/m^2, P = primary productivity/m^3, P′ = primary productivity/m^2, Z = zooplankton, Sp = phytoplankton species, O = oxygen, N = nitrate, N′ = nitrite, N″ = ammonia, Pp = phosphate, S = silicate, D = mixed layer depth, R = total incident radiation]

Operation	Period	Zones	Type of Data	Source
Weather Station "P"				
cruises 593 to 614	1959 to 1961	33	C C' P P' Z O S R	McAllister, 1962
cruises 615 to 634	1961 to 1963	33	CC′ P P' Z O S R	Stephens, 1964
cruises 635 to 655	1964 to 1966	33	C P Z O N R	Stephens, 1966
cruises 661 to 674	1966 to 1967	33	C P O N R	Stephens, 1968
cruises 681 to 706	1968 to 1970	33	C P N R	Stephens, 1970
Ships of Opportunity				
cruises 02 to 43	1968 to 1972	15,19,20,22-34,36-42	C P Sp N Pp S D R	Anderson, unpubl.
	1958			
BROWN BEAR 199	June to July	20,32,37	O Pp D	Fleming, 1959
H.M. SMITH 46	Aug. to Sept.	24,25,29,30,31,38,39,40	C P Z O	McGary and Graham, 1960
VITYAZ 29	Oct. to Dec.	19-21,24,27,29,30,32,35,37,41,42	P Z N Pp R	Koblentz-Mishke, 1969
	1959			
OSHORO MARU 44	June	22,25,29	zoPp	Faculty of Fisheries, 1960
BROWN BEAR 235	Julyto Aug.	15,19,20,23,24,27,28,34,36	coPp	Stephens, 1964
	1960			
OSHORO MARU 46	June to Aug.	18-20,22-24,29-32,35,37,38	spzoPps	Faculty of Fisheries, 1961. Motoda and Kawamura, 1963
	1961			
OSHAWA 1961	June	19,33,36,37	CONS	Antia et al., 1962
OSHORO MARU 048	June	22,29	Z	Faculty of Fisheries, 1962
PIONEER 66	Sept. to Oct.	22,23,26,29,30,38,39,42	CPZ	Doty, 1964
	1962			
OSHAWA 1962	April	42	CNS	Antis et al., 1962
	1964			
G. B. REED 164	Jan. to Feb.	19,20,21,24,27,28,31-37,42	C	Stephens, 1964
AGASSIZ Ursa Major	Aug. to Sept.	16,24,27,31,40	C Sp Z O N' Pp S	University of California, 1967. Venrick, 1969.
	1965			
OSHORO MARU 014	June	22,24,25,29	Z	Faculty of Fisheries, 1966
	1966			
ARGO Zetes I	January	16,24,27,31,40	CPhSpZONN′ Pp S	University of California, 1970. Venrick, 1969.
Straits of Georgia	Feb. to Sept.	20	C P N N' N" Pp S	Fulton et al., 1967
KELEZ 166	March	22,25,29	cc′ P P' Z Pp S D R	Larrance, 1971b
Saanich Inlet	May to July	20	C P Z N N' Pp S	Stephens, et al., 1967

Table 4. (continued)

	1966 (cont.)			
PARAGON ?-66		22,25,29	CC′ P P' Z Pp SDR	Larrance, 1971b
KELEZ 366	September	20,22,29-32,37,38	C C' P P' Z N Pp SDR	Larrance, 1971b
	1967			
KELEZ 167	Jan. to Feb.	23,26,30	CC′ P P' Z N Pp SDR	Larrance, 1971b
T.G. THOMPSON 012	Feb. to Mar.	17-19,24,27,28,34-36	CC′ P P' O N Pp S	Anderson, unpubl.
KELEZ 367	April	19,20,36,37	C D	Larrance, 1971b
KELEZ 567	June to July	16,22-25,29	CC′ P P' Z N Pp SDR	Larrance, 1971b
KELEZ 667	July	22	C C' P P' Z N Pp SDR	Larrance, 1971b
KELEZ 767	August	22,25,29	CC′ P P' Z N Pp SDR	Larrance, 1971b
	1968			
KELEZ 268	May	23,26,30	C C' Pp S D	Larrance, 1971b
OSHORO MARU 028	June to July	17,18,22	zoPp	Faculty of Fisheries, 1969
	1969			
ENDEAVOUR Trans Pacific	March to April	20,29-32,37	C P P' Z Pp N S D R	Anon, 1970
VITYAZ 045	May to June	17,18,23,35	CPP′	Anon, 1973
HAKUHŌ MARU 694	August	31	C SP	Takahashi et al., 1972 Asaoka, unpubl.
	1970			
HAKUHŌ MARU 702	May	19,32,34,37,41	O N N' Pp S	Horibe, 1971
OSHORO MARU 037	June to July	16,17,18,22-24,27,31-34,36,37	C Z Pp N N' S	Faculty of Fisheries, 1972
	1971			
T.G. THOMPSON 059	May to June	20,22,23,25,26,27	CC′ O N N" Pp S	Anderson, unpubl.
ACONA cruises 113,117, 122,125	May to Dec.	17	C C′ P P′ Ph Ph′ Sp O N N" Pp S	Goering, Shiels, and Patton (1973) Goering, Patton, and Shiels (1973)
	1972			Hood and Patton (1973)
ACONA 128, 131	March to April	17	C C′ P P′ Ph Ph′ Sp O N N" Pp S	Muench and Nebert (1973) Homer et al., 1973.
T.G. THOMPSON 072	September	24,27,31,40	CC′ P P' Ph Ph' O N N' N" Pp S R	Anderson, unpubl.
	1973			
T.G. THOMPSON" 082	August	32,33,41	CC′ Ph Ph' O N N' N" Pp S R	Anderson, unpubl.
	1974			
HAKUHŌ MARU 742	May	29	C O N N' N" Pp S	Kuroki, 1975
T.G. THOMPSON 091	July	36	C Ph	Anderson, unpubl.

with Thompson, 1952). Conversion of laboratory values to chlorophyll *a* concentration is based on equations which correct for interference from chlorophylls *b* and *c*. Revised equations by UNESCO (1966) produce chlorophyll *a* concentrations which are 24% lower than values derived from the original equations (Banse and Anderson, 1967). To obtain comparable data, we have reduced all data (prior to 1962) based on the equations of Richards with Thompson (1952) or Strickland and Parsons (1960) by 24%. Data based on the equations of Parsons and Strickland (1963) were assumed compatible with data based on the UNESCO equations (Banse and Anderson, 1967). Although later editions of Strickland and Parsons (1965, 1968, 1972) printed both the Richards equations and the Parsons-Strickland equations, in all cases the original data were based on the Parsons-Strickland equations so that data obtained after 1963 did not need reduction.

Chlorophyll *a* concentrations derived from the fluorometric technique (Lorenzen, 1966) were assumed to be comparable with those derived from the spectrophotometric technique.

In the cases where chlorophyll data were reported at depth but integration over the water column was not performed, we have performed that integration. Chlorophyll *a* was integrated down to the one percent light depth by the least squares method. A minimum of two chlorophyll values per station was required for integration. If there were data above and below the one percent light depth, the program interpolated the chlorophyll value at the one percent light depth. If there were no data at or below the one percent light depth, - chlorophyll at this depth was set equal to zero.

Phaeopigments were determined fluorometrically using the method of Lorenzen (1966).

Phytoplankton species: All cell counts compiled were observed in samples collected from water bottles. Counts and proportions taken from net samples were not compiled. All cell counts were obtained using the inverted microscope method of Utermöhl (1931) which depends upon sedimentation to concentrate the cells. Biomass estimates for individual species were computed from cell carbon using the following conversion from plasma volume (Strathmann, 1967):

$$\log c\ (pg) = 0.610 + 0.892 \log (\text{plasma vol} + 0.1\ \text{vacuole vol}).$$

Plasma volume was derived from cell measurements and geometric formulae for 18 cell shapes (Larrance, 1964) assuming a standard plasma thickness of 1 mμ.

Primary prediction: Primary production is most commonly measured using the radioactive carbon uptake method of Steemann Nielsen (1952). Steemann Nielsen's original method involved incubation of phytoplankton samples under standardized (fluorescent)light conditions. Many researchers in the subarctic have continued to use this method (Faculty of Fisheries, 1960, 1961, 1969, 1972). The "in situ" and "simulated in situ" incubation methods are modifications of Steemann Nielsen's method. According to Koblentz-Mishke (1961) data from the standardized light incubation method ("tank" method) are not comparable with those from "in situ" and "simulated in situ" incubations. Therefore, we have compiled only productivity values which have been obtained from incubation in daylight either "in situ" or using neutral density filters on matched depth samples. Productivity values obtained from incubation in an artificial light source (tank method) from composite samples, from depth samples incubated without filters, and from surface samples incubated with filters have not been included.

Carbon assimilation rates which were originally reported as mg $C/m^3/day$ (RV VITYAZ 029) were converted to mg $C/m^3/hr$ by dividing by the number of hours between sunrise and sunset. Hours of daylight were taken from the 1976 Nautical Almanac.

Nutrients: Reactive nitrate was commonly reduced to nitrite, the concentration of which was then determined colorimetrically. Reduction methods [Mullin and Riley, *1955a;* Morris and Riley (Strickland and Parsons, 1972); Wood, Armstrong and Richards, 1967] have varied to improve sensitivity and ease of measurement. We have compiled values from all methods without adjustment.

Because the nitrite concentration is usually a small proportion of the nitrate concentration, we have included the early nitrate data with later data from which nitrite concentrations have been subtracted. Both early and later measurements have been averaged to analyze geographic and temporal variation in nitrate concentrations.

Reactive nitrite was determined calorimetrically according to the method of Benschneider and Robinson (Strickland and Parsons, 1972).

Ammonia was oxidized to nitrite according to the method of Richards and Keltsch (Strickland and Parsons, 1972). This method measures amino acids along with the ammonia.

Reactive phosphate was determined using four methods [Robinson and Thompson (Strickland and Parsons, 1969); Wooster and Rakestraw, 1951; King *et al.*, 1957; Murphy and Riley, 1962]. All four methods utilize a phosphomolybdate complex but differ in rapidity and speed of analysis.

Silicate was determined using two methods [Mullin and Riley, 1955b; Chow *et al.* (Strickland and Parsons, 1972)]. Concentrations of phosphate reported from the VITYAZ 029 cruise were converted from mg m^{-3} to μgm. at. ℓ^{-1} during compilation.

One percent light depth: In cases where the one percent light depth was not reported with the original data, it was calculated from secchi depth by the following formula:

$$I_z = I_o e^{-kz}$$

$$I_z/I_0 = .01$$

$$k = 1.7/\text{secchi depth} \quad \text{(Poole and Atkins, 1929)}$$

$$z_{1\%} = 2.7' \times \text{secchi depth}$$

Secchi depth: For stations which included chlorophyll profiles but not integrated chlorophyll values or one percent light depths, it was necessary to assign a one percent light depth so that the chlorophyll data could be integrated. This was accomplished by locating the station closest in space and time from another cruise and assigning that secchi depth. One percent light depth was then calculated from the secchi depth.

Mixed layer depth: Mixed layer depth, if it was not originally recorded, was taken to be the depth to the top of the major thermocline for thermoclines with a gradient >1°C/15 meters (Giovando and Robinson, 1965). In most cases, the thermocline could be determined from a visual inspection of the temperature profile. If it was not clear, a graph was drawn. When no temperature gradient greater than 1°C/15 meters was observed, mixed layer depth was taken to be the depth to the top of the halocline. In a few cases where temperature inversions were observed (TGT 059 sts. 41, 38, 53) mixed layer depth was taken to be the depth to the top of the pycnocline.

Light level: Light levels which were originally presented as Langleys/half day (VITYAZ 029) were multiplied by 2 to obtain Langleys/day.

Data analysis

The study area was defined as the Subarctic. Pacific east of 180°W and north of 42°N, not including the Bering Sea. The area was divided into 28 geographic zones (Figure 25) based on the work of Dodimead *et al.* (1963). Dodimead *et al.* (1963) divided the Subarctic into domains on the basis of temperature, salinity, and flow characteristics, not on the basis of water masses. The domains exhibited consistent structure and oceanographic behavior. The Central Subarctic Domain displays a permanent halocline at about 100 meters and salinities of 32.4 to 32.8 °/$_{oo}$ in the upper zone. The Transition Domain is warmer and separated

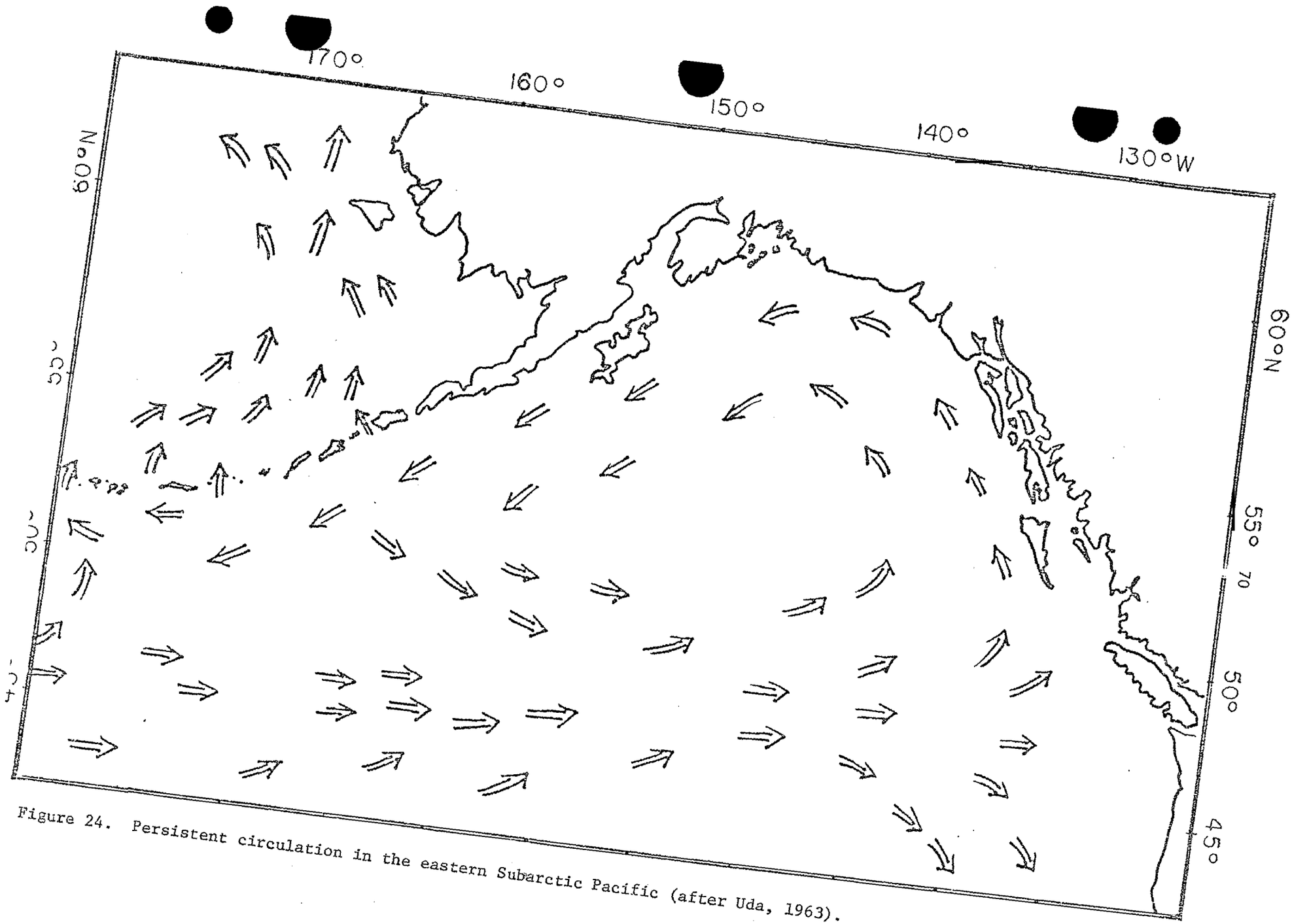


Figure 24. Persistent circulation in the eastern Subarctic Pacific (after Uda, 1963).

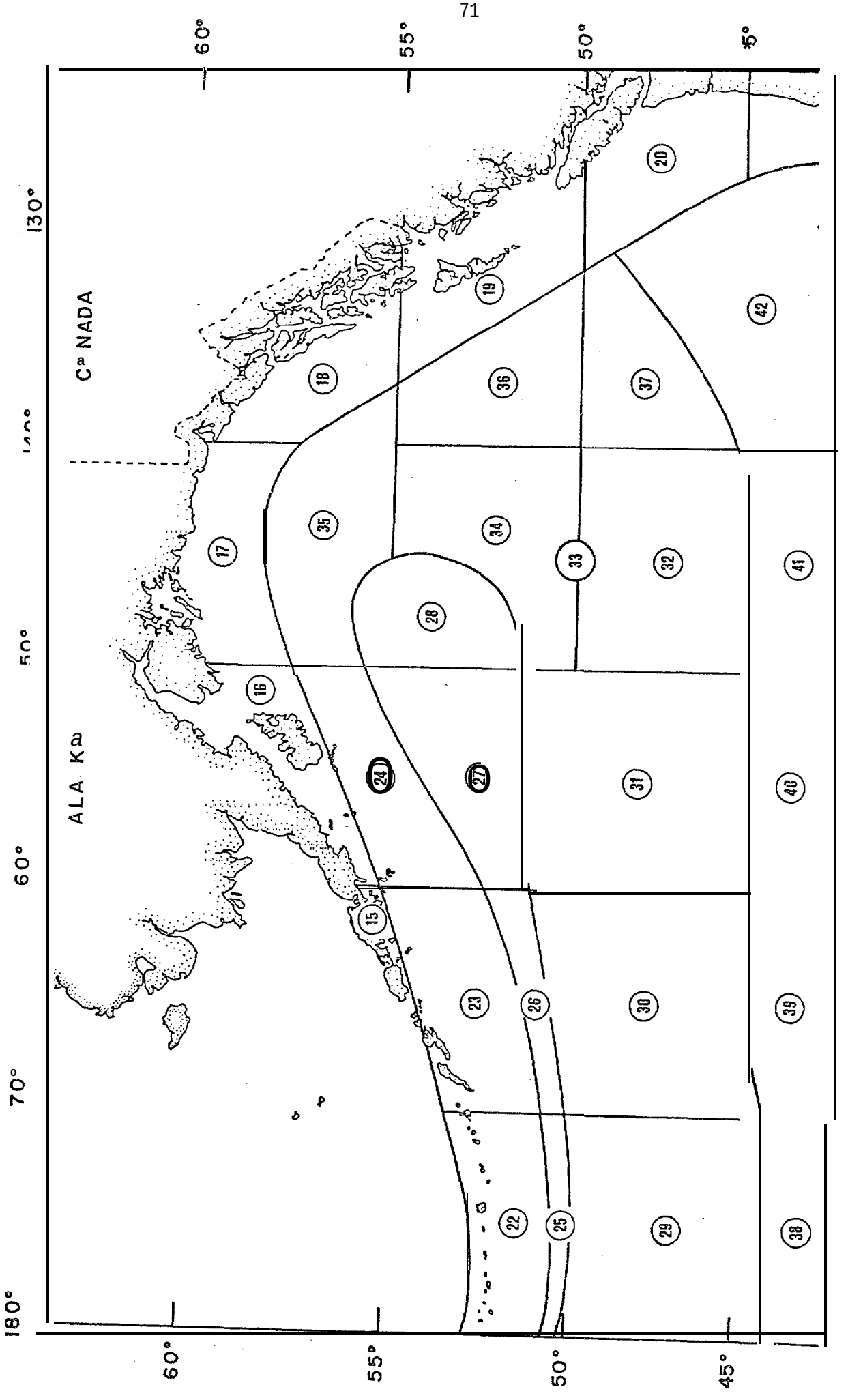


Figure 25. The geographical zones of the eastern Subarctic Pacific. The circled number in each zone is the number by which that zone is identified in the text and in the following figures and tables. Zone 33 is Ocean Weather Station 'P' and its near environs.

from the Central Subarctic Domain by the 7°C isotherm at the bottom of the upper zone. The Coastal Domain is less saline and separated from the Central Subarctic Domain by the isohaline of 32.4 $^{0}/_{00}$ at the surface. The Alaskan Stream Domain is both warmer and less saline than the Central Subarctic Domain, comprising waters with salinities less than 32.6 $O/_{00}$. The Alaskan Gyre is differentiated by flow characteristics and a salinity maximum of 32.8 to 33.1 $'/_{00}$ at the surface. The extensions of the three peripheral domains on the Central Subarctic Domain vary annually. Figure 216 in Dodimead *et al.* (1963), which represents the average positions of the boundaries between domains, was used to define the geographic zones in the present study. Zones 15-21 in the Coastal Domain (Figure 25) include the continental shelf as well as oceanic areas in close proximity to the shelf. Zones 22-24 in the Alaskan Stream Domain include the Alaskan Stream as well as the neritic area of the Aleutian chain. Zones 27-28 define the center of the Alaskan Gyre. Zones 29-31 comprise the Central Subarctic. Zone 33 includes Ocean Weather Station "l?. Zones 32-37 include waters of mixed origin within the Central Subarctic Domain. Zones 29-42 include Transition waters.

The data were divided by season. According to Parsons and LeBrasseur (1968), during March the depth of the mixed layer at Station "P" equals the critical depth as defined by Sverdrup (1953). Parsons and LeBrasseur (1969) predict from physical data that the spring increase in phytoplankton production will occur in March in zones 16, 20, 24, and 42 of Figure 25. Therefore, spring was not defined astronomically in the present study but as the period from March to May. Similarly, summer included June to August; autumn included September to November, and winter included December to February. Station locations for each season are plotted in Figures 26 to 29.

The data were grouped into six depth ranges: 0-10 m, 10.1-25 m, 25.1-50 m, 50.1-100 m, 100.1-150 m, >150 m.

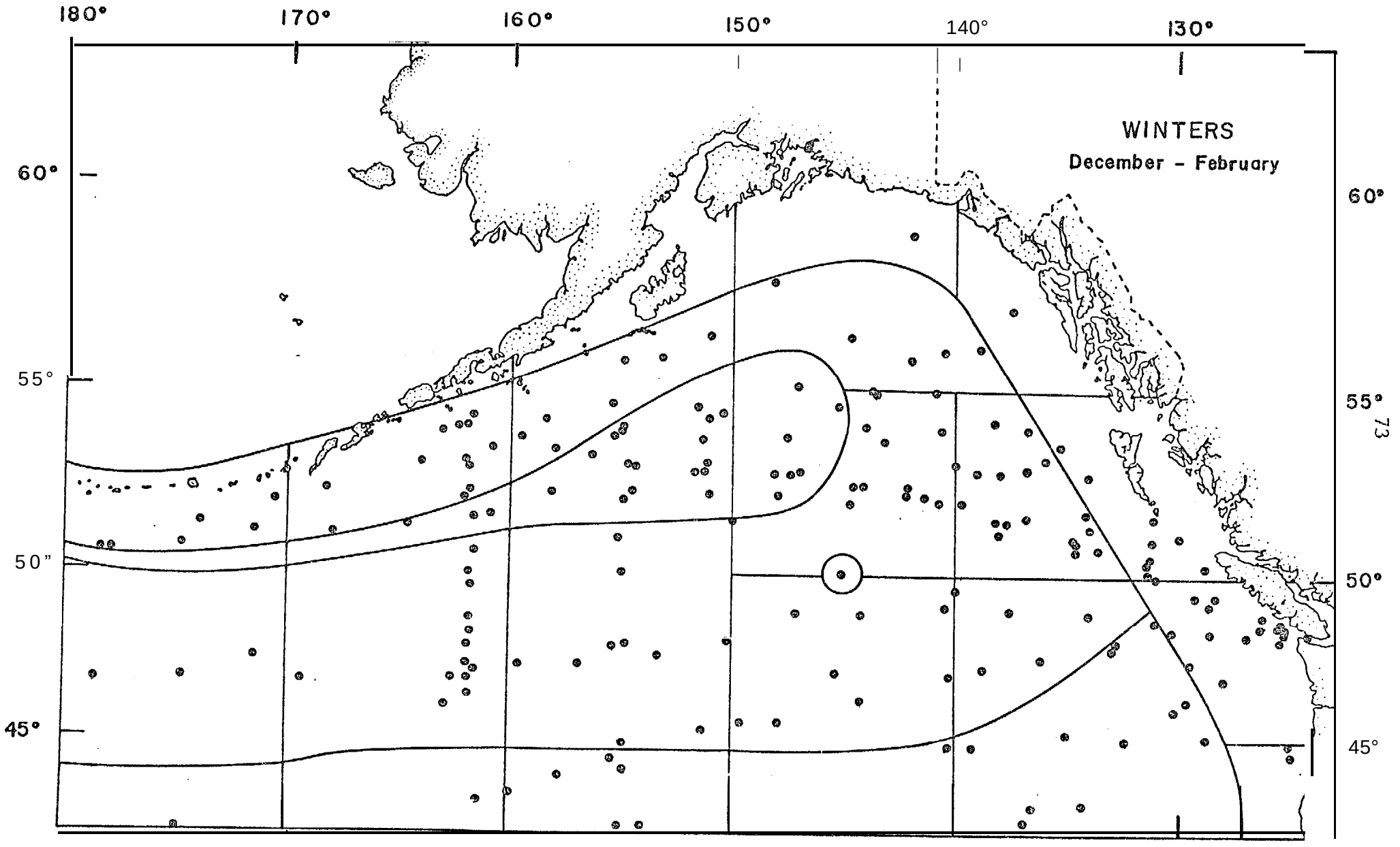


Figure 26. The distribution of stations in the eastern Subarctic Pacific from which data were collected during one or more winters from 1958 through 1974.

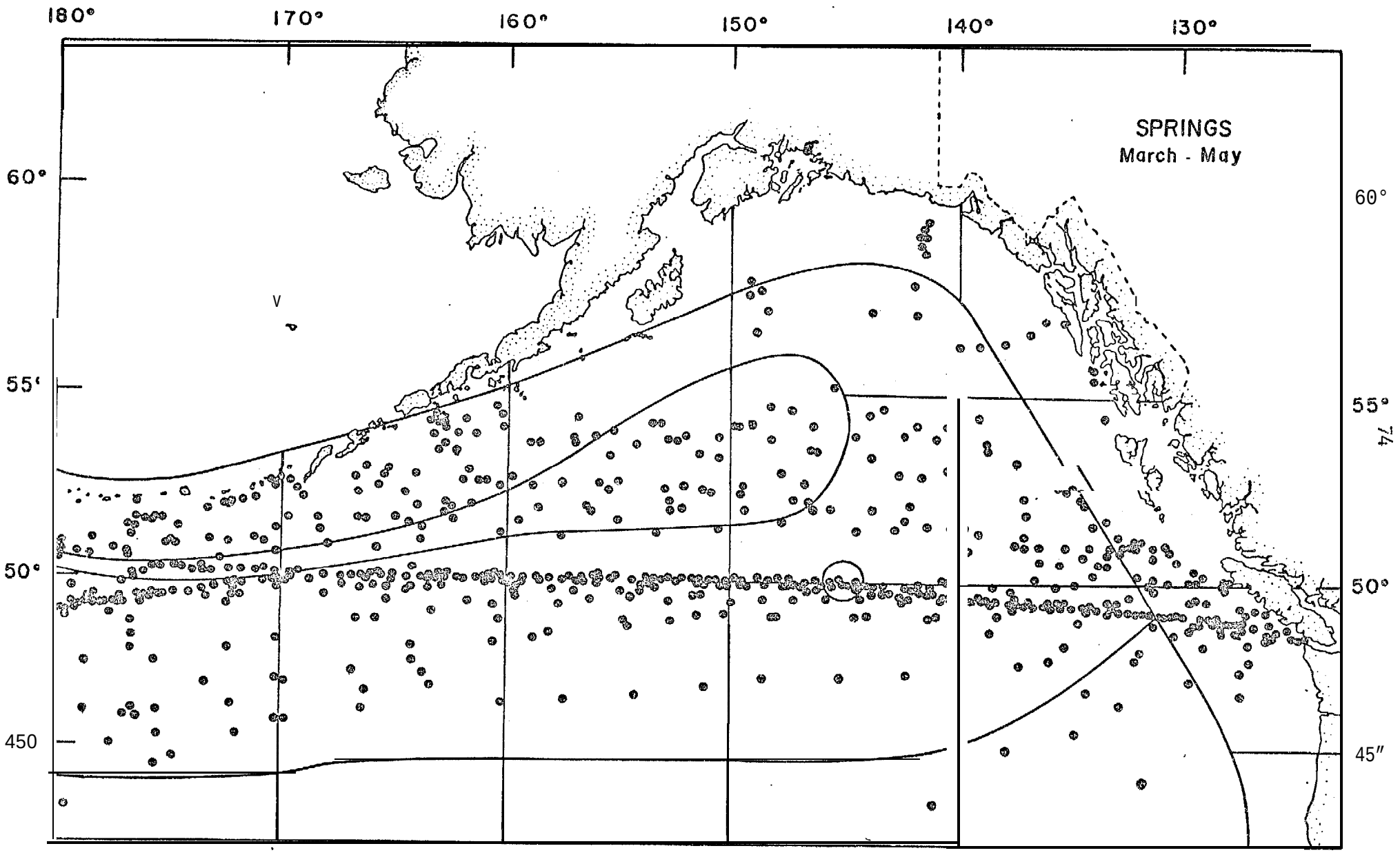


Figure 27, The distribution of stations in the eastern Subarctic Pacific from which data were collected during one or more springs from 1958 through 1974.

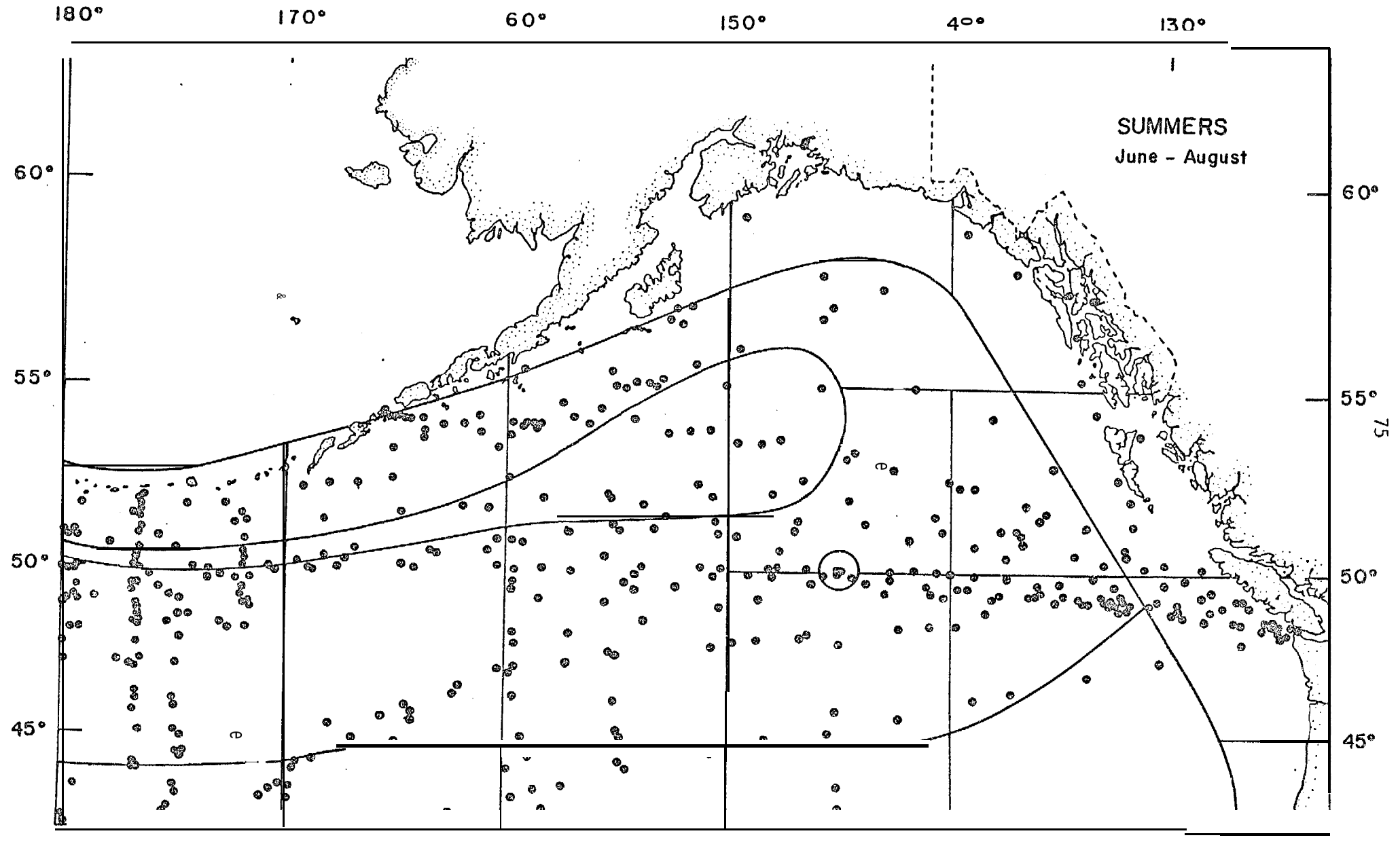


Figure 28. The distribution of stations in the eastern Subarctic Pacific from which data were collected during one or more summers from 1958 through 1974.

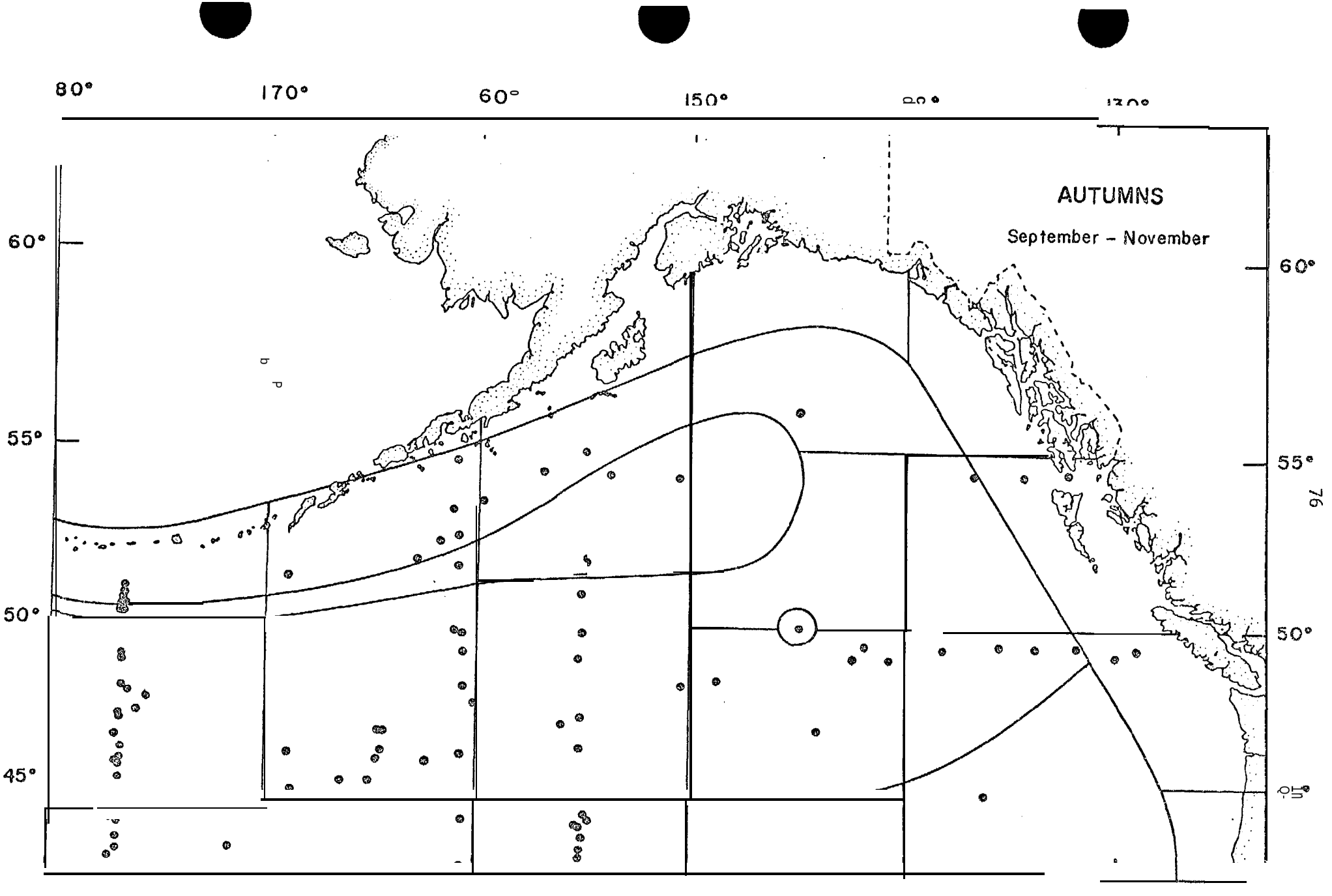


Figure 29. The distribution of stations in the eastern Subarctic Pacific from which data were collected during one or more autumns from 1958 through 1974.

Productivity data: Within each cell formed by one geographic zone, one year, one season, and one depth, the range, mean, and standard deviation for each variable were computed:

$$\text{mean: } \bar{X} = Xi. / n_i$$

$$\text{standard deviation: } s = \frac{\Sigma X_{ij}^2 \quad X_i^2./n_i}{n_i - 1}$$

One-way *analysis* of variance (ANOVA) was used to test the difference between years. The generalized ANOVA table for samples of unequal sizes (Snedecor and Cochran, 1967) is as follows:

Source of Variation	Ss	Degrees of Freedom	Mean Square	Expected Mean Square
Between years	$\Sigma\frac{X_{i\cdot}^2}{n_i} - \frac{X_{\cdot\cdot}^2}{N}$	a - 1	Sc^2	$\sigma^2 + n_0\sigma_A^2$
Within years	$\Sigma\Sigma X_{ij}^2 - \Sigma\frac{X_{i\cdot}^2}{n_i}$	a(N - 1)	S^2	σ^2
Total	$\Sigma\Sigma X_{ij}^2 - X_{\cdot\cdot}^2/N$	N - 1		

where $X_{.ij}$ denotes the jth observation from the ith year, $X_{i\cdot}$ denotes the cell total of the X_{ij} , $x_{\cdot 0} = \Sigma X_{i\cdot}$ denotes the grand total, a denotes the number of years, $'_i$ denotes the size of the sample in the ith cell, and $N = \Sigma n_i$ denotes the total size of all cells. The F ratio, Sc^2/s^2 has (a - 1) and (N - a) degrees of freedom. Mathematically, the model may be written:

$$'_{ij} = \mu + \alpha_i + \varepsilon_{ij}, \quad i = 1 \ldots a, j = 1 \ldots n,$$

Equal cell sizes were impossible to achieve because of the nature of the sampling process. To achieve equal cell size, zonal boundaries would have had to be adjusted. Because each cruise measured different variables (Table 4), the boundaries would have to be different for each variable, a premise which

violated the experimental design. Therefore, unequal cell size was accepted as an undesirable but necessary part of the program.

Although equal cell size is not essential for the performance of single fact-or ANOVA (Zar, 1974), independence of error and variance homogeneity are essential (Sokal and Rohlf, 1969). With unequal cell size, the F-test and t-tests are more affected by non-normality and heterogeneity of variances than with equal cell size (Snedecor and Cochran, 1967). To evaluate independence of error, the variance of each cell was plotted against the mean of the cell for each variable. The Student-t test was used to determine if the resulting regression line differed significantly from zero:

$$t = \frac{b - 0}{S_b}, \text{ d.f.} = n - 2$$

where b = the slope of the regression line, S_b = sample standard deviation of the regression coefficient. Regression was tested at the 95% level for 14 variables (Table 5).

In the cases where the slope of the regression line differed significantly from zero (i.e., the variance was dependent upon the mean), various transformations of the original data were made and the significance of the regression tested again at the 95% level. Transformations which removed dependence are listed in Table 6. The $\sqrt{X}$ transformation was performed on phaeopigments (mg/m^3), ammonia, mixed depth, total radiation. The $\sqrt{X+1}$ transformation was performed on nitrate. The $\log_{10}(X+1)$ transformation was performed on integrated chlorophyll *a* (mg/m^2). No transformation was necessary for phosphate, silicate, nitrite, integrated phaeopigments, integrated productivity, or integrated zooplankton. No transformation could be found for chlorophyll *a* (mg/m^3), primary productivity ($mg\ C/m^3/hr$) or oxygen which would achieve independence.

Table 5. Regression of cell variance on cell mean for 14 variables in the Eastern Subarctic Pacific

Variable	b[1]	S_b[2]	b/S_b	d.f.	'95
Chlorophyll a	3.76	0.23	16.64**[3]	167	1.98
Integrated chlorophyll a	128.83	20.22	6.37**	57	2.00
Phaeopigments	0.77	0.07	10.35**	3	3.18
Integrated phaeopigments	4.06	3.00	1.36	30	2.04
Nitrate	1.07	0.52	2.04*[4]	142	1.98
Phosphate	-0.06	0.13	-0.45	181	1.98
Silicate	0.57	0.45	1.25	157	1.98
Nitrite	0.16	0.19	0.85	18	2.10
Ammonia	0.56	0.20	2.82*	15	2.13
Oxygen	-0.08	0.03	-2.37*	57	2.00
Depth of mixed layer	5.11	1.96	2.61*	198	1.98
Incident radiation	29.45	6.93	4.25**	209	1.98

1) b = slope of regression line

2) S_b = sample standard deviation of the regression coefficient

3) significant at the 99% level

4) significant at the 95% level

Table 6. Regression of cell variance on cell mean for 7 transformed variables in the Eastern Subarctic Pacific

Variable	Transformation	b [1]	$'_b$ [2]	b/S_b	d.f.	t
Integrated chlorophyll a	$\log_{10}(X+1)$	0.02	0.16	0.13	57	$'_{50} = 0.68$
Phaeopigments	$\sqrt{X}$	0.81	0.30	2.68	3	$'_{95} = 3.18$
Nitrate	$\sqrt{X+1}$	0.0003	0.05	0.007	142	$t_{50} = 0.68$
Ammonia	$\sqrt{X}$	0.042	0.09	0.48	15	$'_{50} = 0.69$
Depth of mixed layer	$\sqrt{X}$	0.096	0.13	0.74	198	$'_{60} = 0.84$
Incident radiation	$\sqrt{X}$	0.32	0.17	1.93	209	$'_{95} = 1.97$

1) b = slope of regression line

2) $'_b$ = sample standard deviation of the regression coefficient

After the appropriate transformations were made, the ANOVA program was run and the difference between years evaluated. The results are outlined in Tables 7 and 8. F-ratios based on samples from 2 or more years where only one year had more than 2 samples were considered invalid, and the results were left out of the analysis.

When a large number of ANOVA tests are performed at the 95% level, 5% of the tests are expected to be positive (i.e., the null hypothesis is rejected) when in fact the null hypothesis is true. This is termed a Type I error; it overestimates a difference. The proportion of positive F-tests to the total valid tests performed was computed for each variable at each depth range (Table 9). The proportions for each variable far exceed 5/100, thereby indicating real differences between years. Type II errors cause an underestimation of real differences and so do not need to be considered here.

Finally, all the years were averaged, and the range, mean, and standard deviation were computed for each variable in each geographic zone at each depth for each season. The results are plotted in Figure 27 to 74 and listed in Appendix A.

Phytoplankton species data: Phytoplankton species data were insufficient to allow analysis of seasonal variation; therefore, samples collected between January and June for all years were analyzed for geographic variation. Only surface samples were analyzed to provide comparability with the large body of Ships-of-Opportunity data. Stations within each geographic zone were grouped together. The number of stations sampled in each zone are indicated in Figure 75. For each species occurring within each zone, six statistics were computed:

1) Mean number of cells per liter. The cell concentration of the species was averaged over the samples in which that species occurred,

Table 7. Geographic zones in the Eastern Subarctic Pacific which show significant variation between years (tested at the 95% level).

Variable	Season	0-10m	10-25m	25-50m	50-100m	100-150m	>150m
Nitrate[1)]	Winter	20[2)],27,31,32,36	--	--	27	33	--
	Spring	19,20,22,25,29-34,37	33	--	20,33	33	33
	Summer	20,23,27,31-34,37	33,37	20,32,33	20,32,33	33	33
	Autumn	33	--	--	--	--	33
Phosphate	Winter	20,27,31,32,36	--	--	--	--	--
	Spring	20,22,25,29-32,36,37	22,25	20,22	20	--	--
	Summer	23,25,29,31,32,33,38	20,22,29>32	20,29,33,37,38	22,29	29,33	24,27,29,31,38
	Autumn	--	--	--	40	--	--
Silicate	Winter	20,32,34,36,40	--	--	27	--	--
	Spring	20,22,25,29-32,34,37	22,30	20,22,29,30	20,29,30	--	--
	Summer	20,22,23,25,27,29,31-34	19	20,29,31-33	20,29,31,33	--	22,29
	Autumn	40	--	40	--	--	--

1) ANOVA performed on $\sqrt{X+1}$ transformation of data

2) Zone 20 (see Figure 25)

Table 8. Geographic zones in the Eastern Subarctic Pacific which show significant variation between years (tested at the 95% level).

Season	Integrated chlorophyll a[1)]	Depth of Mixed Layer[2)]	Incident Radiation[2)]
Winter	33[3)]	--	30, 33
Spring	23, 33	20, 22	22, 33
Summer	33	20, 22, 29, 32	--
Autumn	29, 33	--	33

1) ANOVA performed on $\log_{10}(X+1)$ transformation of data

2) ANOVA performed on $\sqrt{X}$ transformation of data

3) Zone 33 (see Figure 25)

Table 9. Ratio of positive F-tests to total tests performed for analysis of variance between years in the Eastern Subarctic Pacific.

Variable	0-10m	10-25m	25-50m	50-100m	100-150m	>150m
Nitrate	25*/39**	3/5	3/4	6/10	2/4	3/4
Phosphate	21/38	6/10	7/13	4/11	2/3	5/7
Silicate	25/27	3/6	10/12	8/11	0/3	2/3

Integrated chlorophyll a	6/7
Depth of mixed layer	6/24
Incident radiation	5/10

* 23 instances of significant difference between years

** 39 valid ANOVA tests performed

2) Maximum percentage of total cells. In each sample the percentage contribution of the species to the total phytoplankton cell count was determined. The maximum percentage within each zone was the highest percent contribution at any one station.

3) Mean carbon per liter. In each sample the cell concentration of the species was multiplied by the estimated amount of carbon per cell to produce an estimate of the biomass (in nanograms carbon per liter) of the species. The mean for each zone was the biomass of the species averaged over the samples in which the species occurred.

4) Maximum percentage of total carbon. In each sample the percentage contribution of the species to the phytoplankton biomass was determined. The maximum percentage within each zone was the highest percent contribution at any one station.

5) Number of stations present. The number of occurrences of the species within the zone was counted.

6) Percentage occurrence. The number of occurrences of the species was divided by the total number of samples within the zone and multiplied by 100.

Phytoplankton species were ranked in importance according to the number of occurrences, according to the maximum cell concentration at any one station, according to the maximum percent contribution to cell numbers at any one station, according to the maximum biomass at any one station, and according to the maximum percent contribution to biomass at any one station. All neritic stations were omitted so that the rankings would indicate the relative importance of species in the oceanic Subarctic.

D. Results

Productivity data

Annual variation: Significant annual variation during all seasons was observed for every variable on which valid ANOVA tests could be performed (Tables 7 and 8). Annual variation of nitrate, silicate, and phosphate was most frequent in the upper 10 meters and for the spring and summer seasons. The results indicate, however, only zones where annual variation could be demonstrated. Not all the blank spaces in Tables 7 and 8 indicate annual homogeneity; for many of them the sample number was insufficient for analysis of variance. Zones where valid ANOVA tests supported annual homogeneity are listed in Tables 10 and 11.

Preliminary analysis of variance tests performed on untransformed chlorophyll a data indicate extensive annual variation. Chlorophyll a variation is best documented in zone 33 (Figure 30). A general upward trend of average chlorophyll a concentrations occurs from 1965 to 1969. Variation of chlorophyll a within years is greatest in the summer months. Annual variation between 1960 and 1965 at Station "P" has been described by Wickett (1973).

Chlorophyll a: Mean chlorophyll a concentrations show little seasonal change in the surface layer of the eastern oceanic Subarctic Pacific, in contrast to the marked seasonal variation of neritic zones (15, 17, 18, 20) (Figure 27). The neritic influence extends well beyond the shelf break, however, as evidenced by an average spring chlorophyll a concentration of over 2 mg m^{-3} in zone 25 and a summer average over 1 mg m^{-3} in zone 36. In most zones spring averages were higher than summer averages with the exception of zones 20, 26, 32, and 36, where summer averages were higher. A summer maximum is also suggested in Transition waters (zones 38, 41, 42), but the data are too few to be conclusive. Comparison of seasonal means within the oceanic area (zones 26 to 42) shows a small but significant difference (at the 99 percent level) between winter and spring, between spring and autumn, and between summer

Table 10. Geographic zones in the Eastern Subarctic Pacific which show no significant variation between years (tested at the 95% level)

Variable	Season	0-10m	10-25m	25-50m	50-100m	100-150m	≥150m
Nitrate[1)]	Winter	22,23,30,33,34,40	33	--	*33*	33	3
	Spring	23,27,28,36,42	--	32	*29,32*	--	--
	Summer	22,29,36	--	--	--	--	--
	Autumn	--	23	--	*33*	33	--
Phosphate	Winter	22,23,30,34,40	--	--	*27*	--	--
	Spring	19,23,27,28,34	23,30	29,32	*29,30,32*	--	--
	Summer	20,22,27,34,36,37	31,37	22,24,31	31,32,33,38	--	22,25
	Autumn	40	--	40	--	40	--
Silicate	Winter	22,23,27,30,31	--	--	--	--	--
	Spring	19,23,27,28,36,42	23	32	32	32	--
	Summer	36,37	22,29	22	22	29,32	27
	Autumn	--	--	--	40	40	--

1) ANOVA performed on $\sqrt{X+1}$ transformation data

2) Zone 20 (see Figure 25)

Table 11. Geographic zones in the Eastern Subarctic Pacific which show no significant variation between years (tested at the 95% level).

Season	Integrated Chlorophyll *a*	Mixed Depth Layer	Incident Radiation
Winter	--	30,36	--
Spring	--	19,22,23,27,28,29, 30,31,32,34,36,37	23,29
Summer	31	31,33,34	29,33
Autumn	--	29	29

Table 12. Seasonal variation in average surface chlorophyll *a* concentrations in the eastern oceanic Subarctic Pacific (zones 26 to 42*).

Season	Number of Observations	Maximum (mg m^{-3})	Mean (mg m^{-3})	σ^2	t'
winter	291	1.37	0.305	0.0165	
					9,69 ($p < .01$)
spring	532	2.16	0.424	0.0506	
					3.28 ($p < .01$)
summer	561	1.97	0.370	0.1022	
					3.18 ($p < .01$)
autumn	360	1.25	0.316	0.0354	

* See Figure 25

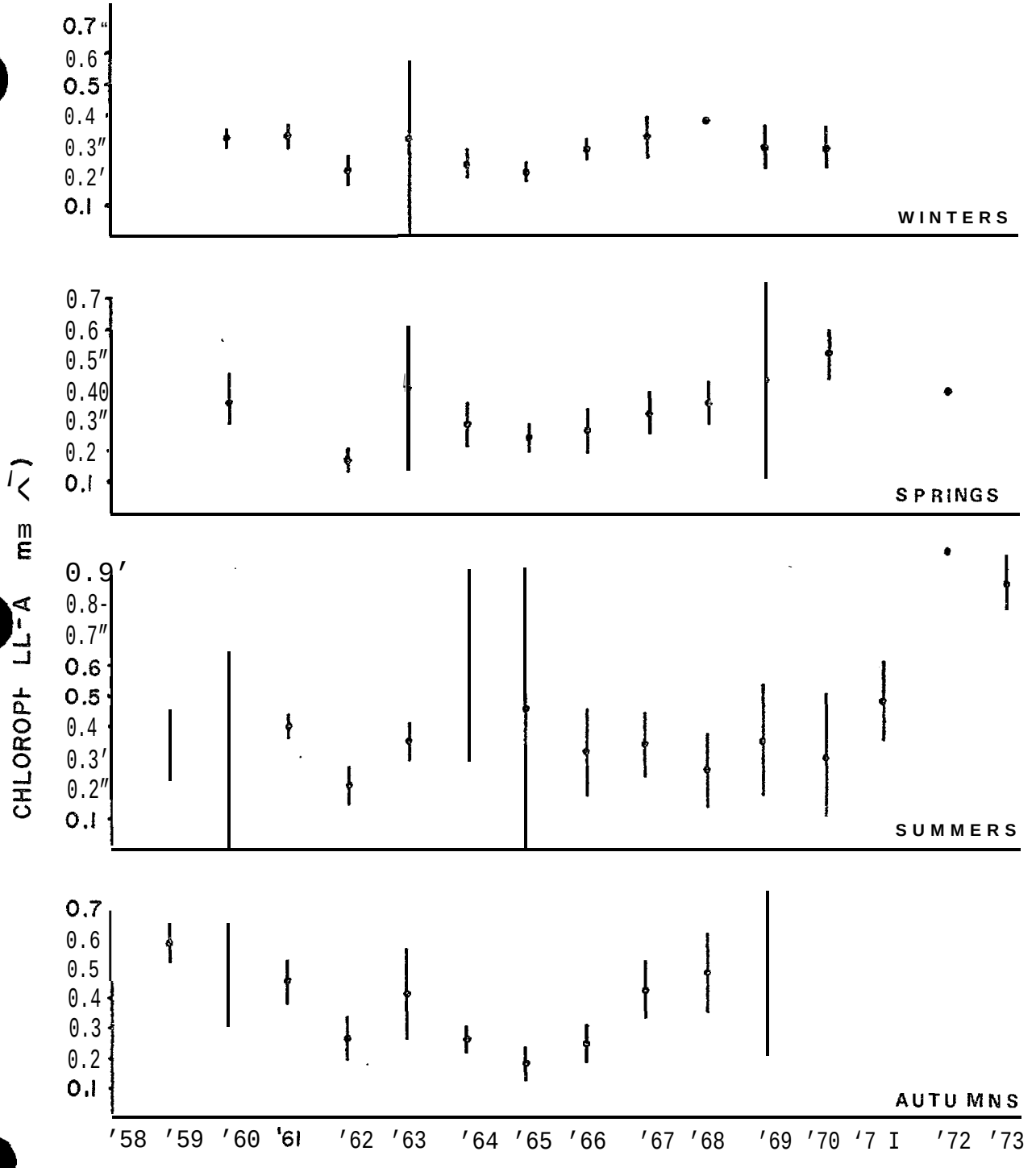


Figure 30. Chlorophyll a (mean seasonal concentration ± standard deviation) at Ocean Weather Station 'P' (145°W, 50°N) from 1959 to 1973.

and autumn (Table 12). Surface characteristics in all zones are constant (uniform) to 50 m (Figures 28, 29) except in zone 17, where consistently low chlorophyll a values occur below .25 m. The summer maximum in zone 20 is consistent in all three depth interval-s to 50 m. Below 50 m, chlorophyll a concentrations are lower than those above 50 m, and no seasonal variation is apparent with the exception of zones 20 and 22 (Figures 30, 31, 32). The variation of surface chlorophyll a over an eleven year period at Station "P" is plotted in Figure 1. Intra seasonal variation of chlorophyll a at depth is greatest during summer months and the first month of autumn in zone 33 (Figure 2).

The seasonal and geographic distribution of chlorophyll a integrated over the euphotic zone is similar to that of discrete chlorophyll a concentrations in the upper 50 m (Figure 33). Seasonal variation occurs in neritic areas (zones 17, 20, 22, 23, 24) and in oceanic areas south of the Aleutians (zone 25). The summer maximum in integrated chlorophyll a in zone 24 (Figure 33), which is indicated also in discrete chlorophyll a concentrations between 10 and 50 m (Figures 28, 29) is based on too few data to be conclusive. Zone 24 includes neritic stations which may produce a seasonal pattern similar to zone 20.

Primary production: Primary production in surface waters peaks in summer in oceanic zones (Figure 34) and in spring in neritic zones where high. production is maintained throughout the summer. A similar contrast of oceanic and neritic zones occurs at 10 to 25 meters depth (Figure 35). Below 25 m production is low in spring in neritic zones and in summer in oceanic zones (Figure 36) when standing stock increases in the upper layers reduce the depth of the photic layer. Productivity below 50 meters was negligible in all zones and was not plotted; the values are available in Appendix A. Productivities integrated over the euphotic zone demonstrate patterns similar to the discrete values in zones 17 and 33. Other zones contain too few data to warrant any conclusions.

Nutrients: Surface nitrate concentrations in the oceanic Subarctic build up during winter and spring and decrease between spring and summer (Figure 38). In contrast, nitrate concentrations in neritic areas (zones 17, 19, 20) peak in winter and decrease steadily from winter to summer. The difference can be attributed to a delayed phytoplankton growth period caused by late formation of a seasonal thermocline in the oceanic areas (Parsons and LeBrasseur, 1969). Oceanic areas experience another decrease in nitrate concentrations between summer and fall, while neritic areas (zones 17, 20) experience an increase. The neritic increase can be explained by regeneration and mixing in shallow water.

Average nitrate concentrations approach zero values in neritic areas in summer (Figure 38) but remain well above limiting concentrations in oceanic areas. The difference has been attributed to the shorter growth period in oceanic areas (Parsons and LeBrasseur, 1969) and to low oceanic phytoplankton biomass resulting from grazing (McAllister *et al.*, 1960) as discussed in Anderson *et al.*, (1369). Discrete nitrate concentrations of zero do appear in summer in neritic zones (see Appendix A for minimum values). Average values are consistently higher in all seasons in the Alaskan Gyre (zones 27, 28) and lower in Transition waters (zones 38 to 42). Mixed waters (zone 37) are intermediate between Central waters (zones 29-33) and Transition waters.

Surface concentrations of phosphate and silicate duplicate both the seasonal and geographic distributions of nitrate (Figures 44, 50). Average phosphate concentrations do not drop as low as nitrate concentrations even in the neritic and Transition areas, suggesting that nitrate probably is a limiting nutrient in those areas. Discrete summer concentrations of phosphate do, however, drop to zero in zone *17 (see* Appendix A). Silicate concentrations

are low in zone 17 at all seasons, decreasing to limiting amounts in spring. Zero values of silicate occur in spring in zone 17 and in summer in zones 20, 23, 36, 37, and 40 (see Appendix A). Spring silicate concentrations in zone 29 are not as high as those described by Park *et al.* (1968) who found values to 30 µgm at ℓ^{-1}, while phosphate concentrations are in the range they found.

Nitrate concentrations at depth follow surface patterns, both seasonally and geographically to 100 meters (Figures 39, 40, 41). Some zones (27, 31) develop a summer nitrate maximum which is intensified below 100 meters (Figure 42). This subsurface nitrate maximum can be explained by regeneration in the waters lying between the seasonal thermocline and the halocline (50-150 m). Concentrations below 100 m are higher in all zones including Transition waters (Figure 46). The autumn increase in zone 20 is greatest from 10 to 100 m. Intra seasonal variation in nitrate in zone 33 is greatest between 100 and 150 m (Figure 4).

Phosphate concentrations at depth follow surface patterns to 25 meters (Figure 45). Below 25 meters, seasonal variation is reduced in the central zones (Figures 46, 47, 48, 49) and a summer phosphate maximum develops in zone 17, which contrasts with the seasonal pattern in other neritic zones. This effect is explained by the fact that most zone 17 data were collected well inshore in Port Valdez, whereas other neritic zones were sampled over the shelf. Between 100 and 150 meters, a summer maximum also occurs in zone 20, suggesting regeneration at depth. Below 150 meters, phosphate concentrations in Transition and mixed waters (zones 32, 34, 37, 38, 40, 41) show a sizable decrease between spring and autumn (Figure 49) in contrast to the 100-150 meter interval. General levels of phosphate are higher below 150 meters.

Silicate concentrations at depth resemble the nitrate pattern (Figures 51 to 55). Concentrations in zone 17 drop to zero in summer between 10 and 50 meters (Figures 51, 52). The summer decrease in mixed waters below 150 meters follows nitrate and phosphate patterns (Figure 55).

Oxygen concentrations above 100 m show little seasonal change in oceanic zones (Figures 56 to 59). Decreased oxygen solubilities due to temperature increases are balanced by photosynthetic increases in spring resulting in little change from winter to spring. A summer reduction due to reduced volubility is seen in most zones. A spring maximum caused by photosynthesis and *a* summer minimum in zone 17 are found at all depths. The spring maxima found below 100 meters in zones 24 and 27 (Figure 60) are anomalous values based on only 2 samples. Sizeable changes in oxygen concentrations from spring to autumn in zones 29 to 40 are based on too few data to be conclusive (Figure 61).

Ammonia concentrations rise in the spring (Figures 62, 63) and increase or decrease in summer and autumn in zones 17 and 20. Transition waters (zones 40, 41) have low ammonia concentrations above 25 meters and greater amounts from 25 to 100 meters (Figures 62 to 67). Below 50 meters, ammonia falls to zero in zones 20, 24, 27, 31.

Nitrite data (Figures 68-72) are too few and too conflicting (compare the upper depth intervals in zones 17, 20) to provide useful conclusions. Nitrite concentrations seem to become negligible below 150 m (Figure 72).

Physical factors: The seasonal pattern of daily radiation is best documented in zone 33 (Figure 73). Light limitation in autumn months is apparent. Oceanic areas in the central Subarctic demonstrate the same pattern. Increased cloud cover in summer (Dodimead and Tully, 1958) can explain the low summer radiation values in zones 22 and 29. No north-south variation can be

demonstrated, verifying Dodimead and Tully (1958}, but the southern zones show higher incident radiation in autumn and winter.

Seasonal variation in the depth of the mixed layer is best documented in zone 33 (Figure 74) where the maximum occurs in winter (85.8 meters) and the minimum in summer (18.5 meters). An autumn increase occurs in the areas east of 150°W but not west of 150°W. Because the seasonal thermocline decays between September and November, early autumn samples would bias an average depth. It it probable that the western areas show such a bias. The deepest winter mixing depth occurs in the western area (zone 30) and the shallowest in the Alaskan gyre (zone 28). These conclusions are in agreement with those of Giovando and Robinson (1965).

Discussion: Despite the broad scope of the experimental design, which averages across three month periods and wide depth intervals, the results are consistent within variables and between variables. For instance, surface patterns in nutrient concentrations are consistent for several depth intervals within individual zones (i.e. , nitrate in the upper 50 meters in zone 17). Furthermore, three principal nutrients (nitrate, phosphate, silicate) show similar patterns within individual zones (i.e., surface values in zone 24) and inverse patterns when compared with oxygen' (i.e., zone 27 at 100 to 150 meters). These consistent patterns point to real events as opposed to artifacts of the sampling and averaging programs. ' Seasonal patterns which are based on few data points can be confirmed by comparison with patterns in adjacent zones which were sampled more thoroughly (i.e., compare the mixing depth in zones 32 and 33 (Figure 74).

Respectively higher nutrient concentrations at all depths in the Alaskan gyre demonstrate the doming or upwelling process described by Uda (1963) and Anderson *et al.* (1969). Uda (1963) furthermore notes high transparencies in the gyre which indicate lack of plant growth. The present study does not

confirm any difference between the Alaskan gyre (zones 27 to 28) and other Central Subarctic areas with respect to chlorophyll a concentrations (Figure 27) or primary production (Figure 34). Shoaler mixed depths are demonstrated for both the Alaskan gyre and Station "??" which is close to the gyre axis. Venrick (1969) found low nutrient, phytoplankton, and zooplankton concentrations at the gyre axis as well as high diatom equitability. She suggests a stable regime which is in contradiction to the hydrography. The present study finds physical and chemical affirmation of upwelling with no apparent effect on biological features.

Phytoplankton species data

Out of 121 Ships-of-Opportunity samples, Thai.ass<os~~a *lineata* occurred 118 times. *Nitzschia* sp. (Pseudonitzschia group), *Fragilariopsis pseudonana*, *Denticula seminae*, and *Coccolithus huxleyi* were found in over 75% of the samples (Table 13).

Cell concentrations of over 100,000 cells/liter were achieved by *Nitzschia pseudonana*, while *Denticula seminae*, *Rhizosolenia alata* f. *inermis*, *Nitzschia* sp. (*Pseudonitzschia* group), *Corethron hystrix*, *Cylindrotheca closterium*, *Cyclococcolithus* sp. B, *Coccolithus huxleyi* occurred in concentrations over 10,000 cell/liter (Table 14). The same species contributed over 20% to total cell numbers (Table 14), but the rank order differed from that based on maximum cell numbers.

A maximum biomass over 10 µgm carbon/liter was reported for *Corethron hystrix*, *Rhizosolenia alata* f. *inermis*, *Ethmodiscus rex*, *Asteromphalus* spp.-, and *Denticula seminae* (Table 14). Over 50% of total phytoplankton carbon at some stations was contributed by *Gyrodinium* spp., *Corethron hystrix*, *Ethmodiscus rex*, *Rhizosolenia alata* F. *inermis*, *Ceratium pentagonum*, and *Cyclococcolithus* sp. B (Table 14).

Table 13. Phytoplankton species rankings according to five criteria using data from 121 Ships-of-Opportunity Samples.

Species	No. of Occurrences	Mean no. cells/ℓ	Max. % of total cells	Mean carbon/R	Max % of total carbon
Centric diatoms					
Actinoptychus undulatus	60[1)]	69	56	70	53
Asteromphalus spp.	12	12	4	14	20
Bacteriastrum mediterraneus	50	48	50	42	57
Biddulphia spp.	59	54	23	62	27
Cerataulina sp.	53	61	63	59	64
Chaetoceros atlanticus	16	14	22	17	34
C. convolutes	10	15	8	10	12
C. peruvianus	36	40	46	46	63
Corethron hystrix	11	5	1	5	2
Coscinodiscus centralis	42	51	47	61	59
C. curvatulus	37	49	31	48	49
C. lineatus	17	33	43	25	46
C. oculus iridis	38	58	10	54	43
C. radiatus	30	53	41	44	32
C. stellaris	30	34	11	31	17
Dactyliosolen mediterraneus	32	25	36	20	38
Ditylum brightwellii	44	16	19	40	25
Ethmodiscus rex	62	75	3	72	3
Eucampia zoodiacus	57	72	64	69	61
Hemiaulus sinensis	62	77	70	74	68
Lauderia borealis	48	73	32	63	26
Leptocylindrus danicus	62	39	61	39	66
Planktoniella sol	57	76	62	75	65
Rhizosolenia alata	29	50	45	53	36
R. alata f. curvirostris	24	29	26	26	16
R. alata f. inermis	22	3	2	4	4
R. hebetata f. hiemalis	31	63	37	64	44
R. hebetata f. semispina	35	25	40	33	50
R. stolterfothii	43	30	20	41	30
R. styliformis	46	23	18	29	21

1) Species is 60th on list ranked by number of occurrences, where 1st occurs most often.

Table 13 continued

Species	No. of Occurrences	Mean no. cells/2	Max. Z of total cells	Mean carbon/ℓ	Max. % of total carbon
Skeletonema costatum	55	17	54	18	48
Stephanopyxis nipponica	49	64	51	49	58
Thalassiosira condensata	61	45	53	47	56
T. decipiens	21	21	28	22	42
T. eccentrica	21	38	12	27	15
T. lineata	1	10	25	15	24
T. nordenskioeldii	45	9	17	11	23
T. pacifica	56	31	35	38	51
T. rotula	48	13	21	13	29
T. *subtilis*	62	47	67	50	75
Pennate diatoms					
Asterionella japonica	56	67	73	68	74
Cylindrotheca closterium	19	6	34	7	11
Denticula seminae	4	2	5	3	7
Licmophora abbreviate	62	44	52	60	69
Navicula spp.	15	43	60	35	40
Nitzschia longissima	32	35	59	28	45
Nitzschia pseudonana	3	1	25	1	18
Nitzschia sp. (*Fragilariopsis* group)	9	16	58	12	60
Nitzschia sp. (*Pseudonitzschia* group)	2	4	27	6	37
Pseudoeunotia doliolus	54	19	68	71	73
Rhabdonema arcuatum	18	27	55	34	62
Thalassionema nitzschioides	26	36	48	32	52
Thalassiothrix longissima	13	22	6	16	22
Tropidoneis antarctica polyplasta	14	20	13	21	14
Dinoflagellates					
Ceratium fusus	39	68	38	57	33
C. longipes	50	62	29	73	31
C. *macroceros*	47	70	33	65	28
C. *pentagonum*	28	65	15	56	5
C. tripes	48	71	39	66	35

Table 13 continued

Species	No. of Occurrences	Mean no. Cells/k	Max. % of total cells	Mean carbon/ℓ	Max. % of total carbon
Dinophysis acuta	41	52	42	43	47
Gymnodinium spp.	7	28	30	24	19
Gyrodinium spp.	5	18	14	19	1
Miniscule bipes	40	74	72	67	71
Peridinium depressum	25	37	16	37	10
P. cerasus	22	41	44	36	41
Coccolithophorids					
Calyptrosphaera spp.	36	55	71	55	70
Coccolithophorid "C"[3)]	45	56	65	30	55
Coccolithus huxleyi	6	8	9	8	8
C. pelagicus	8	11	25	9	13
Cyclococcolithus Sp. A[1)]	33	32	49	23	39
*C.*sp. B[2)]	29	7	24	2	6
Syracosphaera spp.	52	66	69	58	7
Rhabdosphaera tignifer	51	60	66	52	67
Silicoflagellates					
Dictyocha fibula	20	26			
Distephanus octangulatus	34	59			
Other groups					
Pterosperma sp.	27	57	57	45	54
Halosphaera viridis	23	42	7	51	9

1) *Cyclococcolithus* sp. 'A' resembles *Cyclococcolithus leptoporus*

2) *Cyclococcolithus* Sp. 'B' resembles *Cyclococcolithus fragilis*

3) *Coccolithophorid* 'C' resembles *Michaelsarsia* sp.

Table 14. Phytoplankton species from 121 Eastern Subarctic stations (neritic stations omitted) ranked according to 4 criteria.

Rank	Species	Max. no. cells/ℓ	Rank	Species	Max. carbon/ℓ
1	*Nitzschia pseudonana*	7.06×10^5	1	*Corethron hystrix*	7.73×10^4
2	*Denticula seminae*	8.26×10^4	2	*Rhizosolenia alata f. inermis*	4.37×10^4
3	*Rhizosolenia alata f. inermis*	5.12×10^4	3	*Ethmodiscus rex*	1.59×10^4
4	*Nitzschia* sp. (*Pseudonitzschia* group)	4.29×10^4	4	*Asteromphalus* sp.	1.21×10^4
5	*Corethron hystrix*	4.16×10^4	5	*Denticula seminae*	1.00×10^4
6	*Cylindrotheca closterium*	3.34×10^4	6	*Thalassithrix longissima*	7.75×10^3
7	*Cyclococcolithus* sp.B	2.84×10^4	7	*Halosphaera viridis*	6.62×10^3
8	*Coccolithus huxleyi*	1.74×10^4	8	*Chaetoceros convolutus*	5.36×10^3
9	*Thalassiosira nordenskioe ldii*	1.14×10^4	9	*Coccolithus huxleyi*	4.83×10^3
10	*Thalassiosira lineata*	9.33×10^3	10	*Coscinodiscus oculis iridis*	3.38×10^3
11	*Coccolithus pelagicus*	7.77×10^3	11	*Coscinodiscus stellaris*	3.12×10^3
12	*Asteromphalus* spp.	6.22×10^3	12	*Thalassiosira eccentrica*	2.98×10^3
13	*Thalassiosira rotula*	5.72×10^3	13	*Tropidoneis antarctica polyplasta*	2.74×10^3
14	*Chaetoceros atlanticus*	5.26×10^3	14	*Gyrodinium* spp.	2.58×10^3
15	*Chaetoceros convolutes*	5.07×10^3	15	*Ceratium pentagonum*	2.48×10^3
16	*Nitzschia* sp (*Fragilariopsis* group)	4.37×10^3	16	*Peridinium depressum*	2.33×10^3
17	*Skeletonema costatum*	3.33×10^3	17	*Thalassiosira nordenskioe ldii*	2.12×10^3
18	*Gyrodinium* spp.	2.91×10^3	18	*Rhizosolenia styliformis*	1.92×10^3
19	*Pseudoeunotia doliolus*	2.58×10^3	19	*Ditylum brightwelli*	1.70×10^3
20-	*Tropidoneis Antarctica* var. *polyplasta*	2.42×10^3	20	*Rhizosolenia stolterfothii*	1.62×10^3

Table 14 continued

Rank	Species	Max. % of total cells/i	Rank	Species	Max. % of total carbon/ℓ
1	*Nitzschia pseudonana*	85.4	1	*Gyrodinium* spp.	85.7
2	*Cyclococcolithus* sp. B	54.2	2	*Corethron hystrix*	75.5
3	*Denticula seminae*	38.5	3	*Ethmodiscus rex*	64.4
4	*Rhizosolenia alata f. inermis*	32.2	4	*Rhizosolenia alata f. inermis*	61.4
5	*Corethron hystrix*	24.9	5	*Ceratium pentagonum*	57.2
6	*Nitzschia* sp. (*Pseudonitzschia* group)	24.8	6	*Cyclococcolithus* sp. B	50.s
7	*Cylindrotheca closterium*	24.3	7	*Denticula seminae*	44.7
8	*Coccolithus huxleyi*	21.5	8	*Coccolithus huxleyi*	44.2
9	*Coccolithus pelagicus*	10.7	9	*Halosphaera viridis*	42.8
10	*Chaetoceros convolutus*	10.4	10	*Peridinium depressum*	41.3
11	*Thalassiosira nordenskioeldii*	9.8	11	*Cylindrotheca closterium*	40.5
12	*Nitzschia* sp. (*Fragilariopsis* group)	5.3	12	*Chaetoceros convolutes*	40.0
13	*Thalassiosira notula*	4.9	13	*Coccolithus pelagicus*	40.0
14	*Asteromphalus* spp.	3.7	14	*Tropidoneis antarctica* var. *polyplasta*	32.3
15	*Thalassiosira lineata*	2.6	15	*Thalassiosira eccentrics*	30.8
16	*Thalassiothrix longissima*	2.5	16	*Rhizosolenia alata f. curvirostris*	29.3
17	*Chaetoceros atlanticus*	2.4	17	*Coscinodiscus stellaris*	27.0
18	*Skeletonema costatum*	2.0	18	*Nitzschia pseudonana*	24.3
19	*Gyrodinium* spp.	1.8	19	*Gymnodinium* spp.	21.5
20	*Dactyliosolen mediterraneous*	1.5	20	*Asteromphalus* spp.	21.3
21	*Tropidoneis antarctica* var. *polyplasta*	1.5			

Geographic variation: The geographic distributions of phytoplankton species which occurred in more than 10% of the total surface samples collected in the Eastern Subarctic Pacific are presented in Figures 81 to 142. Generalizations based on each figure would be too lengthy to include here. Taken as a whole, the figures demonstrate the widespread distribution of all members of the Subarctic phytoplankton community. In each major phytoplankton group (i.e., the diatoms, the dinoflagellates, the coccolithphorids, and the silicoflagellates) are a few species which are major contributors *to* the Subarctic community.

The species distributions do not show any clear and consistent biological differences between Subarctic water, mixed water, Alaska gyre water, and Alaskan stream water. Certain species were not found in Transition waters (for" example, *Ceratium pentagonum*, Figure 123, and *Thalassiosira nordenskioeldii*, Figure 107); these species differ, however, from those so defined by Venrick (1971) .

A distinction between oceanic and neritic species cannot be made on the basis of the figures because no obligatorily neritic species have been mapped, a feature which is the result of the very limited number of neritic stations sampled. Many of the neritic species are listed in Table 15. The Hyalochaete group of the genus Chaetoceros (Figure 84) includes a number of species which are neritic (*Chaetoceros debilis, decipiens, lacinosus, didymus, radicans, affinis, brevis, pelagicus, socialis, subsecundus, teres.)*. The Ships-of-Opportunity data do not differentiate these species; hence, they could not be mapped separately.

Another group of major importance which was not differentiated into species in the Ships-of-Opportunity data is the microflagellates. This group of organisms, primarily chrysophytes and cryptophytes, occurred in every sample in dominant numbers (Figure 142).

Table 15. Phytoplankton species occurring infrequently in the eastern oceanic Subarctic Pacific.

Species	Zones of Occurrence	Maximum cells/2	Maximum carbon/ℓ (nanograms)	Maximum % cells/2	Maximum % carbon/E
Actinoptychus undulatus	19*,31,36	50	89	0.04	3.40
Asterionella japonica	15,20,36,37	63	0.62	0.05	0.02
Bacteriastrum mediterraneous	15,19,20,36,37	289	113	0.34	2.35
Biddulphia spp.	15,36,37	204	1570	0.10	15.40
Cerataulina sp.	19,20,24,27,28,36	96	23	0.13	0.78
Ethmodiscus rex	29	18	15900	0.02	64.40
Eucampia zoodiacus	20,31,34,36	41	22	0.05	1.06
Hemiaulus sinensis	36	8	7	0.01	0.47
Leptocylindrus danicus	17,22	49	27	0.46	0.56
Licmophora abbreviata	20	424	100	0.12	0.31
Planktoniella sol	22,29,34,37	17	25	0.007	0.66
Pseudoeunotia doliolus	31,37,40	2580	13	0.03	0.12
Stephanopyxis nipponica	15,20,22,24,34,36,37	82	110	0.19	2.18
Syracosphaera sp.	19,20,24,29,30,31,36	71	8	0.14	0.25
Thalassiosira condensata	20,36	385	97	0.22	2.86
Thalassiosira pacifica	15,19,20,32,37	1230	388	0.47	3.80
Thalassiosira subtilis	37	303	14	0.19	0.02

*Zone 19, see Figure 25.

The widespread occurrence of *Coccolithus huxleyi* (syn. *Emiliania huxleyi)* demonstrated in Figure 133, is supported by Okada and Honjo (1973). The distribution of *Chaetoceros atlanticus* as well as several other species Is in accord with Koblents Mishke {1969).

Species which occur infrequently in the oceanic Subarctic are either warm water species or neritic species. The warm water species on Table 15 are *Ethmodiscus rex, Eucampia zoodiacus, Hemiaulus sinensis, Plantoniella sol, Pseudoeunotia doliolus.* It can be observed that these species occurred in Transition waters or mixed water to the north of the Transition Zone. *Rhizosolenia styliformis* is also a warm water species. Its occurrence around the outside of the gyre (Figure 102) suggests a confirmation of the hypothesis of Ohwada and Asaoka (1963) that traces of warm water are carried along the outer edge of the gyre. The occurrence of *Planktoniella sol* in zone 22 carried the hypothesis to its limit. The remaining species listed in Table 15 are neritic species. Their occurrence in zones 36 and 37 (mixed waters) suggests that these waters can be distinguished from the Central Subarctic zones to the west (Tully *et al.*, 1960). Oceanic species abundant in coastal waters are *Corethron hystrix, Coscinodiscus oculis iridis, Chaetocerosconcavicornis,* and *Rhizosolenia hebatata* (Williamson, 1974).

A list of species recorded from the eastern Subarctic Pacific is presented in Table 16.

Discussion: Past studies of phytoplankton species in the Eastern Subarctic Pacific have either defined specific areas dominated by certain species (for instance the work of Japanese scientists) or grouped species into recurrent groups (Venrick, 1971). Ohwada and Kon (1963) describe the cold water species, *Corethron hystrix* and *Denticula seminae,* flowing south out of the Bering Sea in 1960 through western Aleutian passes, and *Nitzschia seriata* flowing in mixed waters north through eastern passes. The relative positions of the "Denticula"

Table 16. Phytoplankton species reported from the Eastern Subarctic Pacific north of 42°N and east of 180°W.

Diatoms

Achnanthes longipes Ag.	O*	*Cyclotella stelligera* Cl. and Grun.	O
A. sp.	N**	*Cymbella* sp.	O
Actinocyclus curvatulus Janisch	O	*Dactyliosolen meditterraneus* H. Pér.	O
A. sp.	O	*Denticula seminae* (Semina) Simon and Kanaya	O
Actinoptychus undulatus (Bail.) Ralfs	O	*Ditylum brightwellii* (West) Grun.	O
Amphiprora sp.	N	*Ethmodiscus rex* (Wall.) Hendey	O
Asterionella japonica Cl.	O	*Eucampia zoodiacus* Ehr.	O
Asterolampra marylandica Ehr.	O	*Gyrosigma* sp.	N
A. flabellatus (Brèb.) Grev.	O	*Grammatophora marina* (Lyng.) Kütz	O
A. hepactus (Brèb.) Ralfs	O	*Hemiaulus sinensis* Grev.	O
A. robustus Castr.	O	*H. membranaceous* Cl.	O
Bacteriastrum delicatulum Cl.	O	*Hemidiscus cuneiformis* Wall.	O
Bacteriosira fragilis Gran.	N	*Lauderia borealis* Gran.	O
Biddulphia aurita (Lyng.) Brèb. and God.	N	*Leptocylindrus danicus* Cl.	O
B. longicruris Grev.	O	*Licmophora abbreviate* Ag.	O
B. sp.	O	*Melosira moniliformis* (Müll.) Ag.	N
Cerataulina sp.	O	*M. sulcata* (Ehr.) Kütz	N
C. bergonii H. Pér.	O	*Navicula* sp.	O
Chaetoceros atlanticus cl.	O	*Nitzschia seriata* Cl.	O
C. convolutes Castr.	O	*N. sicula* (Castr.) Hustedt	O
C. concavicornis Mang.	O	*N. bilobata* Wm. Smith	O
C. peruvianus Brightw.	O	*N. bicapitata* Cl.	O
C. debilis Cl.	N	*N. heimii* Manguin	O
C. decipiens Cl.	N	*N. turgiduloides* Hasle	O
C. didymus Ehr.	N	*N. longissima* (Brèb.) Ralfs	O
C. lacinosus Schütt	N	*N. pungens* Hasle	N
C. radicans Schütt	N	*N. paradoxa* (Gmel.) Grun.	N
C. affinis Laud.	N	*N. pseudonana* (Steeman Nielsen) Hasle	O
C. brevis Schütt	N	*N.* Sp.	O
C. mitra (Bail.) Cl.	N	*Planktoniella sol* (Wall.) Schütt	O
C. pelagicus Cl.	N	*Pleurosigma directum* Grun.	O
C. socialis Laud.	N	*Podosira* sp.	O
C. subsecundus (Grun.) Hust.	N	*Pseudoeunotia dolidus* (Wall.) Grun.	O
C. teres Cl.	N	*Rhabdonema arcuatum* Kützing	O
Cocconeis sp.	O	*Rhizosolenia alata* Brightw.	O
Corethron hystrix Hen.	O	*R. alata f. curvirostris* Gran	O
Coscinodiscus lineatus Ehr.	O	*R. alata f. inermis* (Castr.) Hust.	O
C. curvatulus Grun.	O	*R. hebetata* **f.** *hiemalis* Gran	O
C. centralis Ehr.	O	*R. hebetata f, seimspina* (Hen.) Gran	O
C. radiatus Ehr.	O	*R. styliformis* Brightw.	O
C. stellaris Rep.	O	*R. styliformis* f. *longispina* Hust.	O
C. oculis iridis Ehr.	O		
C. tabularis Grun.	O		
C. marginatus Ehr.	O		
C. wailesii Gran and Angst	O		
C. granii Gough	N		
C. perforates Ehr.	O		
Cylindrotheca closterium Reiman and Lewin	O		

* oceanic
** neritic

Table 16 continued

Diatoms

R. stolterfothii H. Pér.	O*
R. fragilissima Berg.	O
R. imbricata shrubsolei (Cl.) Schröd.	O
R. obtusa Hensen	O
Roperia tesselata (Roper) Grun.	O
Skeletonema costatum (Grev.) Cl.	O
Stephanopyxis nipponica Gran and Yendo	O
S. *turris* (Grev. and Am.) Ralfs	N**
Striatella unipuntata (Lyng.) Ag.	N
Surirella sp.	N
Synedra vaucheriae Kutz. var. *capitellata* Grun.	O
Thalassionema nitzschioides Grun.	O
Thalassiosira decipiens (Grun.) Jørg.	O
T. *angstii* (Gran.) Makarova	O
T. *nordenskiöldii* Cl.	O
T. rotula Meun.	O
T. pacifica Gran and Angst	O
T. subtilis (Osten.) Gran	O
T. condensata Cl.	O
T. lineata Jousé	O
T. antiqua (Grun) A. Cl. var. *septata* Prosh. Lavr.	O
T. *oestrupii* (Ostf.) Hasle	O
T. eccentrica (Ehr.) Cleve	O
T. polychorda (Gran) Jørg.	O
Thalassiothrix longissima Cl. and Gran	O
Trieeratium arcticum Brightw.	N
Tropidoneis antarctica Grun. var. *polyplasta* Gran and Angst	O

Dinoflagellates

Ceratium fusus (Ehrenb.) Dujardin	O
G'. *longipes* (Bailey) Gran	O
C. *tripes O.* F. Müller	O
C. *macroceros* (Ehr.) Vanhöffen	O
C. *pentagonum* Gourret	O
C. *lineatum* (Ehr.) Cl.	N
C. *intermedium* (Jörg.) Jörg.	O
Dinophysis acuta Ehr.	O
Exuviella baltica Lohmann.	O
Gymnodinium sp.	O
Gyrodinium sp.	O
Miniscule *bipes* Lebour	O
Peridinium depressum Bailey	O
P. cerasus Paulsen	O
P. conicum (Gran) Ost. and Schmidt	N
P. pallidum Ost.	N

Coccolithophorids

Calyptrosphaera sp.	O
Coccolithus huxleyi (Lohm.) Kpt.	O
C. *pelagicus* (Wallick) Schiller	O
Cyclococcolithus leptoporus (Murr. et. Blackm.) Schiller	O
C. *fragilis* (Lohm.) Gaarder	O
Michaelsarsia sp.	O
Rhabdosphaera tignifer Sch.	O
Syracosphaera sp.	O

Other groups

Pterosperma sp.	O
Halosphaera viridis Schmitz	O
mμ flagellates	O
Phaeocystis pouchetii (Hariot) Lagerheim	N
Ebria tripartite (Schum.) Lemmerman	O
Dictyocha fibula Ehr.	O
Distephanus speculum (Ehr.) Haeckel	O
D. octangulatus Wailes	O

* O = oceanic
** N = neritic

and "Nitzschia" communities were different in 1957 (Iizuka and Tamura, 1958) reflecting annual variation. Figures 110 and 1.15 show dominance of these two species in all the Central Subarctic zones, Cupp (1937) documents annual variation in the species *Asterionella japonica*, which was completely absent at Scotch Cap, Alaska (near eastern Aletuian passes) for two years. Two studies distinguish the *Nitzschia* (Pseudonitzschia group) community from the Subarctic community (Ohwada and Ken, 1963; Marumo, 1967) while Venrick (1971) defines three Subarctic communities, one of which includes *Nitzschia*. [This is not a semantic problem. The *Nitzschia seriata* of Japanese works is surely the same species as Venrick's *Nitzschia turgiduloides*. The present study has labelled this species *Nitzschia* sp. (Pseudonitzschia group).]

Recurrent group analysis was performed on the Ships-of-Opportunity data upon which the present study is based. No recurrent groups could be defined within the surface layer (Munson, personal communication). The present study demonstrates that each of the earlier generalizations applies only to the specific time period studied, a conclusion similar to that drawn by Allen (1943) after 20 years of phytoplankton research off southern California.

Distributions of individual species can also be shown to be specific in time and not general for all years. Venrick (1971) found *Denticula seminae*, *Corethron criophilum*, (syn. *Corethron hystrix*), and *Fragilariopsis pseudonana* (syn. *Nitzschia pseudonana*) restricted to the Central Subarctic north of 46°N. Figures 110, *86,* and *113* show all three to occur south of 43°N. [Figures 99 and 117 confirm Venrick's report that *Rhizosolenia hebatata* f. *hiemalis*, and *Thalassionema nitzschioides* do not occur in Transition water.] The distributions of *Thalassiothrix longissima* (Figure 118) and *Tropidoneis antarctica* var. *polyplasta* (Figure 119) are not restricted to the southern Subarctic in contrast to Venrick (1971). Venrick states that the *Nitzschia closterium/longissima*

complex (syn. *Cylindrotheca closterium/Nitzschia longissima*) is rare near the axis of the Alaska gyre. Figures 109 and 112 show uniform distribution of this species across the Subarctic.

The widespread occurrence of *Thalassiosira lineata* across the eastern Subarctic in concentrations of 10000-10000 cells/t is of interest. From her own observations and the work of others, Hasle (1976) describes this species as a warm-water species, although she indicates its occurrence to 55°N. The present study (Figure 106) documents *Thalassiosira lineata* as a major member of the Subarctic community, not a warm-water accidental. Another species, *Pseudoeunotia doliolus*, does seem to be a warm water introduction *as* described by Hasle (1976). This species was recorded once in the Ships-of-Opportunity data in zone 17, confirming its rare occurrence in the Subarctic Pacific. The sizeable concentrations of *Pseudoeunotia doliolus* found by Venrick (1969) to extend to 50°N must have been a rare event.

E. Discussion

The relatively narrow range of variation, both seasonal and geographic, of biological and chemical parameters in the oceanic eastern Subarctic is in contrast to the wide range of annual variation. Phytoplankton species distributions as well as chlorophyll a concentrations, primary production, and nutrient concentrations support this generalization. Annual variation in this context is not seen as a general trend but as a series of biological "events". The "events" do not stand out in averaged data but do appear in the tables of ranges (Appendix A). For instance, the averaged data show a small seasonal change in primary production in surface waters at Station "P" (zone 33), with a summer mean of 3.37 mg $C/m^3/hr$. However, a maximum production rate of 38.20 mg $C/m^3/hr$ has been recorded at Station "P". Such an event cannot mean a low standing stock, growing rapidly, but must mean a sizeable population, growing

fast. In fact, high chlorophyll a concentrations have been reported from Station "P" (maximum: 2.08 mg chl a/m^3). Phytoplankton species distributions indicate that such "events" are not caused by a few species but that a number of species can grow to high cell densities. Nor are the events more likely in any one subdivision of the oceanic area. The data indicate that there are in each phytoplankton group a number of species most successful in the Subarctic Pacific; which species dominates the event must be dependent upon a series of advantageous circumstances prior to the event. Beklemishev and Nakonechnaya (1972) describe blooms of diatoms south of the Aleutians with dimensions of 150 x 420 nautical miles. The factors responsible for the "events" cannot be nutrients, although computing nutrient concentration changes is a good way of monitoring such events. Factors responsible could be a number of sunny days in succession in combination with a shallow mixed layer and grazing pressure lessened due to patch zooplankton distributions or to migrating zooplankton populations. Study of unusual biological events in the eastern Subarctic should be undertaken.

F. Conclusions

Significant annual variation was found at most seasons and depths in most zones for all the variables tested. The fact that annual variation occurs in zone 33 (Station "P") where a standardized technique and sampling program produces a more balanced experimental design argues against the conclusion that the variation observed was an artifact of the experimental program.

Seasonal variation was also demonstrated for all variables tested, and it was more apparent in neritic zones than oceanic zones. Seasonal variation was least in phytoplankton standing stock (as measured by chlorophyll a concentrations) in oceanic areas.

Geographic variation was most apparent between coastal and oceanic areas. Coastal regimes were found to extend well beyond the shelf break south of the Aleutian chain and west of Vancouver Island. Geographic variation within the Central Subarctic Domain could not be distinguished from annual variation except in the gyre axis, which was chemically and physically separate from other Central Subarctic zones. Transition waters were distinct from those of the Central Subarctic for biological and chemical factors as well as for some phytoplankton species.

G. Needs for future study

The scale of the experiment was too broad to delineate any but the most general relationships between physical and biological parameters. Future studies should be concentrated on the biological "events" when phytoplankton standing stock and production rise well above average values. Because nutrients are not limiting in the oceanic Subarctic, upwelling does not explain the "events". The combination of physical and biological factors preceding "events" should be described.

The paucity of data from inshore areas is striking. Now that new OCSEAP data are available, it should be included in the program developed in the present study to fill in some of the gaps. ,

Annual variation in the boundaries of the principal Subarctic domains should be related to biological parameters, and the unusual characteristics of the axis of the Alaskan gyre system should be considered.